



PHD

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**STUDIES ON THE GROWTH AND NUTRITION OF
WATERCRESS *NASTURTIUM OFFICINALE* R.Br.**

**Submitted by S.M. BENNETT
for the degree of Ph.D.
of the University of Bath**

1986

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LIST OF ABBREVIATIONS

id	Internal diameter
k	Conductance
DI	Deionised (water)
DM	Dry matter
DW	Dry weight
FW	Fresh weight
PP	Photoperiod
AAS	Atomic Absorption Spectrophotometry
ARC	Agricultural Research Council
FIA	Flow Injection Analysis
PAR	Photosynthetically Active Radiation
EDTA	Ethylene diamine tetra acetic acid
NNEDD	N-(1-naphthyl)ethylene diamine dihydrochloride
SS	Stock Solution
IS	Irrigating Solution

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ABSTRACT

The environmental control of watercress growth and nutrient uptake was investigated under controlled experimental conditions. Temperature had a strong influence on growth and uptake; the effects were modified according to photoperiod and complex interactions were observed.

Growth and uptake were closely correlated with light intensity in the range studied.

Rate of plant growth was seen to affect nutrient uptake, and N : P : K uptake ratio was a function of growth stage. Measured on the basis of crop area, uptakes of N and K increased as growth progressed, while P absorption remained relatively constant. Measured on a fresh weight basis, uptake of all three nutrients decreased as growth progressed. Uptakes of P and K were dependent on their respective concentrations in the irrigating solution. Nitrate uptake, however, was independent of concentration in the range studied.

Composition of the irrigating solution affects crop growth, and the optimum solution concentration for maximum watercress yield was identified. Nutrient levels were significantly higher than those attainable by the traditional flow-through system of watercress irrigation, and a recirculatory system was proposed to accommodate solution enrichment.

Ratio of N, P and K in the irrigating solution had little effect on plant growth or tissue nutrient status. Optimum ratio requirements, however, were defined as plant dry matter proportions.

Source of nitrogen had a strong influence on watercress growth and tissue nutrient status. Optimum nitrate : ammonium ratio for maximum yield was 3 : 1.

1. GENERAL INTRODUCTION

1.1 Watercress and its Cultivation

Watercress (*Nasturtium officinale* R.Br., syn. *Rorippa nasturtium-aquaticum* (L.) Hayek) is a cruciferous, freshwater, emergent macrophyte indigenous to Great Britain, Europe, North America and parts of Asia. It has been introduced to South Africa, Australia and to New Zealand where it is a serious river weed (Clapham *et al.*, 1962). Its typical habitat (Haslam, 1978) is a moderately fast-flowing, narrow and shallow stream carrying cool, clear water which is rich in calcium carbonate and nutrients; characteristically a small chalk stream.

The plant is a perennial herb with a hollow, branched stem. Leaves are glabrous and pinnate with 1 - 3 pairs of ovate leaflets and a terminal leaflet, larger than the others. Leaf margins are slightly sinuous and stomata are located on the upper leaf surfaces.

Adventitious roots develop exogenously in the leaf axils and growth of these roots is encouraged under conditions of high relative humidity. Seedling roots develop into basal roots which are finer and more branched than adventitious roots.

The basal root system provides anchorage whereas most adventitious roots are free-floating; both root systems participate in nutrient uptake (Cumbus and Robinson, 1977a) and all roots have a well developed aeration system comprising 'lacunae' (Sculthorpe, 1967).

The inflorescence is a short raceme of small flowers *c.* 6 mm diameter, each comprising 4 sepals, 4 petals and 6 stamens. Cross pollination or self pollination may occur according to circumstances (Johnson, 1974), although it is reported (Howard, 1976) that self pollination is preferred. The fruits are borne on slightly upcurved pedicels and each half of the siliqua contains a double row of seeds which are suborbicular, compressed and *c.* 1 mm diameter. The fruits begin to ripen about 2 months after flowering, and after shedding are dried slowly. Ripeness and germination potential are associated with dark brown seed and seed colour is influenced by temperature and relative humidity during storage (Biddington *et al.*, 1983).

Watercress is a popular salad component, flavouring and garnish. It has a crisp texture and rich colour and is high in vitamins and minerals, particularly iron, calcium, phosphorus and vitamins A and C (Paul and Southgate, 1978). The characteristic flavour is due to β -phenylethyl isothiocyanate which was first isolated from watercress in 1899 by Godamer, and flavour intensity (hotness) is a function of sulphur nutrition (Freeman and Mossadeghi, 1972).

Commercial cultivation in the UK dates back to 1808 when the first watercress beds were built in Kent and production was essentially an extension of natural growth in streams. Until the mid 1940s brown cress was the predominant type grown,

Plate I. Watercress under Cultivation.



but it is a sterile hybrid and inability to maintain virus-free stocks led to its decline.

Brown cress (*Rorippa nasturtium-aquaticum* x *microphyllum*) is a triploid ($2n = 48$), obtained by crossing *R. nasturtium-aquaticum* which is diploid ($2n = 32$), with common wild watercress (*R. microphyllum*) which is tetraploid ($2n = 64$) (Howard, 1976).

Green cress (*Nasturtium officinale* R.Br., syn. *R. nasturtium-aquaticum* (L.) Hayek), being fertile, has now totally replaced brown cress, as virus-free stocks can be raised from seed.

A French strain has been selected for late flowering, vigour, leaf size and colour, and this is now cultivated commercially.

The area under cultivation in the UK is currently 93 ha and is confined mainly to the chalk and limestone regions of Hampshire, Dorset, Wiltshire and Hertfordshire. The largest producer (22 ha) is Hampshire Watercress Ltd., who also have an additional area of 4 ha in Portugal, from which they are able to supply high quality watercress throughout the Winter. Year-round production and intensified cultivation methods have increased the productivity and value of the watercress industry, whose turnover in 1985 was £6 million (MAFF, pers. comm.).

1.2 Commercial Practices

Watercress is produced in rectangular gravel beds, levelled to a slight gradient down their length: spring or borehole

water flows across the beds at rates of up to $11 \times 10^3 \text{ m}^3 \text{ ha}^{-1} \text{ day}^{-1}$.

The water, at source, has a constant temperature of 10.5°C and this heat protects the plants from frost damage during the winter. Water depth and flow rate are adjusted according to stage of crop development and prevailing weather conditions (Anon, 1983).

The irrigating water also supplies nutrients for the watercress and the high flow rates used in winter ensure that the crop receives most of its mineral requirements. Phosphorus, however, is usually deficient and is supplied by regular application of phosphatic fertilisers to the bed base.

In summer the water is cool compared to ambient temperatures, so flow rates are slowed down. This, coupled with faster growth, means the plants rapidly deplete nutrients from the water and deficiency symptoms may appear (Thommen and Westlake, 1981).

Recent changes in production techniques have been rapid as progressive growers have taken advantage of technical developments and moved away from the traditional cultivation methods. Productivity has been increased by increasing the number of harvests taken from the beds and production from seed has taken over from the system of stubble regrowth. Besides avoiding the spread of virus (1.1), this means that flower-free, uniform crops can be harvested throughout the summer, and the time between cropping reduced to 3 - 4 weeks.

Plate 2. Seedlings under Mist Irrigation.
Hampshire Watercress Ltd.



Plate 3. Mechanical Harvesting of Marketable Crop.

Hampshire Watercress Ltd.



Seed is pre-germinated for 48 h in a tank of aerated water, then mixed with a synthetic polymer medium and germinated in a mist propagation unit. After 4 - 5 days the seedlings are transplanted into nursery beds under polythene tunnels, at densities of $c. 3 \times 10^4 \text{ m}^{-2}$. When they reach $c. 7 \text{ cm}$ these plants are harvested with a mechanical mower and the cuttings transplanted into cropping beds at densities of $c. 3 \times 10^3 \text{ m}^{-2}$. They root rapidly and when the crop reaches 20 - 25 cm tall, it is mechanically harvested and marketed.

Watercress for the wholesale market is still bunched and supplied in waxed cardboard boxes, but there is an increasing demand for direct sales to supermarket outlets. In this situation the crop is washed, hydrocooled and then prepacked using automated equipment; either into acetate packs or shrink film-covered plastic containers. Most growers have a 5°C cold store and Hampshire Watercress Ltd. also operate a cold chain distribution system using refrigerated transport.

To meet the demands of market outlets, high quality watercress must be available in large quantities all year round. Such intensive production has led to heavy demand on the mineral nutrients in the irrigating water and may exceed its ability to supply them (Thommen and Westlake, 1981).

Hampshire Watercress Ltd. supply additional nutrients to seedlings through the mist irrigation system (Plate 2) and also provide nutrient enrichment in the watercress beds. Levels of enrichment,

however, are dictated by the need to avoid nutrient pollution of outflow streams (Cumbus, 1975; Casey, 1981) rather than being based on the nutrient requirements of the crop.

1.3 Previous Research on Watercress Nutrition

Several workers have studied the nutritional physiology of watercress during the past 50 years and their conclusions are summarised in the following account.

Studies in small experimental beds on commercial holdings determined that watercress efficiently extracts dilute nutrients from the large volumes of water it receives (Barbier and Marcel, 1938). Analysis of the water supply and of plant tissues indicated that levels of nitrate, sulphate and potassium were sufficient, but phosphorus levels were sub-optimal for crop growth.

This observation was supported by Howard and Lyon (1952) and Crisp (1970), and the use of supplementary phosphorus became standard practice in commercial cultivation (Anon, 1983). However, excess application of phosphorus fertilisers can induce severe chlorosis (Marcel and Barbier, 1939).

Nitrate deficiency was identified in the water supplying one watercress holding in Lincolnshire (Hamence and Taylor, 1947) and a drip feed was set up to supplement nitrate levels by $c. 2 \text{ mg dm}^{-3}$. This improved crop growth at the top of the beds but plants near the outflow still showed deficiency

symptoms, and the outflow water contained no detectable nitrate.

Studies by Lyon and Howard (1952), on the mineral composition of waters supplying the main cress-producing areas of England, concluded that the Lincolnshire case was unusual. They found that most irrigating waters were similar in composition, and characterised by high pH values and calcium levels. Levels of phosphorus and iron were low but other major nutrients were considered adequate; concentrations varied little down the length of the bed providing water flow-rate was maintained. The physico-chemical properties of water; temperature, pH and dissolved oxygen and carbon dioxide; did change as it passed down the bed and temperature gradient was found to be the most important factor affecting crop growth.

Large seasonal variations have been reported in the removal of nitrate, phosphate and ammonium by watercress (Vincent and Downes, 1980). Nitrate uptake showed diurnal variations which were closely correlated with changes in the concentration of dissolved oxygen, and nitrate reductase activity was also found to vary on a diurnal basis. Phosphate and ammonium showed no uptake diurnality.

A balance sheet of the flow of water and minerals into and out of a watercress bed (Crisp, 1970) showed that the outflow water contained 14 times more phosphorus than the inlet, and

this was attributed to the application of basic slag to bed bases. High potassium levels recorded in the outflow immediately after application of potassium fertilisers demonstrated the large loss of nutrients following excessive fertiliser applications.

It was suggested that drip feed applications of phosphate and potassium fertilisers would be more economical than direct applications which are rapidly leached away. Use of recirculating solutions was also discussed, but discounted for use on a commercial scale.

The potential use of low volumes of water enriched with nutrients was investigated by Coïc *et al.* (1972). They found it possible to replace the traditional rapid flow of dilute nutrient irrigating water with a slow moving, concentrated solution, providing that some provision could be made for frost protection in Winter.

Source of nitrogen was also studied by Coïc *et al.* (1972), who compared 'all nitrate' with a 6 : 1 nitrate : ammonium treatment. The 'all nitrate' treatment gave higher yields. This contrasts with the findings of Tripier (1984), who found the optimum ratio to be 2 : 1 nitrate : ammonium nitrogen for watercress cultured on Rockwool.

Studies by Cumbus and Robinson (1977a) have determined the relative contributions of the adventitious and basal root

systems in watercress nutrition, and Cumbus *et al.* (1980) have demonstrated the importance of the bed substrate in supplying phosphorus and micronutrients, when previously it was thought that the substrate was of little consequence in nutrient supply (Lyon and Howard, 1952; Shear, 1968). Nitrogen and potassium are supplied by the irrigating water and, whilst nitrogen concentrations were shown to be adequate, potassium levels may be insufficient to allow optimum growth (Cumbus, 1975).

Chlorosis in watercress has been attributed to an imbalance in micronutrients (Cumbus and Robinson, 1977b; Cumbus *et al.*, 1977), and two systems were found to contribute to the observed imbalance:

- i) enhanced absorption of zinc coupled with reduced manganese uptake; and
- ii) iron deficiency caused by the inhibition of iron translocation, resulting from increased levels of phosphorus, zinc and manganese.

Plant tissue analysis was used by Robinson and Cumbus (1977) to establish critical levels of nitrogen, phosphorus and potassium in watercress leaf tissue. These were 5.7% N, 0.54% P and 2.8% K, where the critical level is defined as that which produces 90% of maximum plant yield (Ulrich and Hills, 1967).

Studies by Rothwell (1983) have quantified the nutrient demand of watercress with respect to nitrogen, phosphorus and potassium. In Winter, rates of uptake were *c.* one tenth of those in Summer, and the potassium concentrations usually found in irrigating waters were found to be only one tenth of those required at times of peak growth.

Diurnality was observed in nitrate and potassium uptakes.

Nitrate uptake was most closely correlated with light intensity, phosphate with solution and air temperatures, and potassium with solution temperature.

Shoot nutrient levels were found to be of the order 4.5 - 5.5% N, 0.9 - 1.3% P and 6.5 - 9.5% K.

A flow injection analysis apparatus was used by Rothwell (1983) for his research on nutrient uptake rates, and this equipment allows rapid analyses to be performed on water samples and plant tissue digests.

The present investigation has developed flow injection analysis (FIA) as a research tool in watercress nutritional studies, to provide further information on the nutrient requirements of the crop.

1.4 Aims of the Present Investigation

The aims of this investigation have been to elucidate the crop's nutrient requirements with respect to N, P and K, and to determine the extent to which plant growth and nutrition are controlled by environmental factors, by the plant itself

and by the nutrient composition of the irrigating solution.

Section A investigates the control of growth and nutrient uptake according to environmental conditions and examines the effects of temperature, photoperiod and light intensity.

Section B investigates the intrinsic properties of watercress with respect to its growth and nutrient uptake.

Experiment 4.2 aims to characterise the crop's growth curve in relation to time, and to quantify uptake and plant nutrient status according to stage of growth;

Experiment 4.3 studies the capacity of the plant for N, P and K uptake, using a continuously-depleting solution.

The importance of solution composition in the control of growth has also been considered.

Section C studies nutrient concentration and ratio, to determine their relative contributions to watercress growth. The main aim has been to identify the optimum concentration and ratio for maximum yield.

Section D investigates nitrogen nutrition and aims to quantify the optimum nitrate:ammonium ratio.

These investigations have aimed to provide quantitative data, from which may be deduced a basic understanding of the crop's nutrient requirements. The results obtained under controlled

experimental conditions may then be applied to watercress production in the commercial situation.

2. MATERIALS AND METHODS

2.1 Cultivation Methods

2.1.1 Plant Material

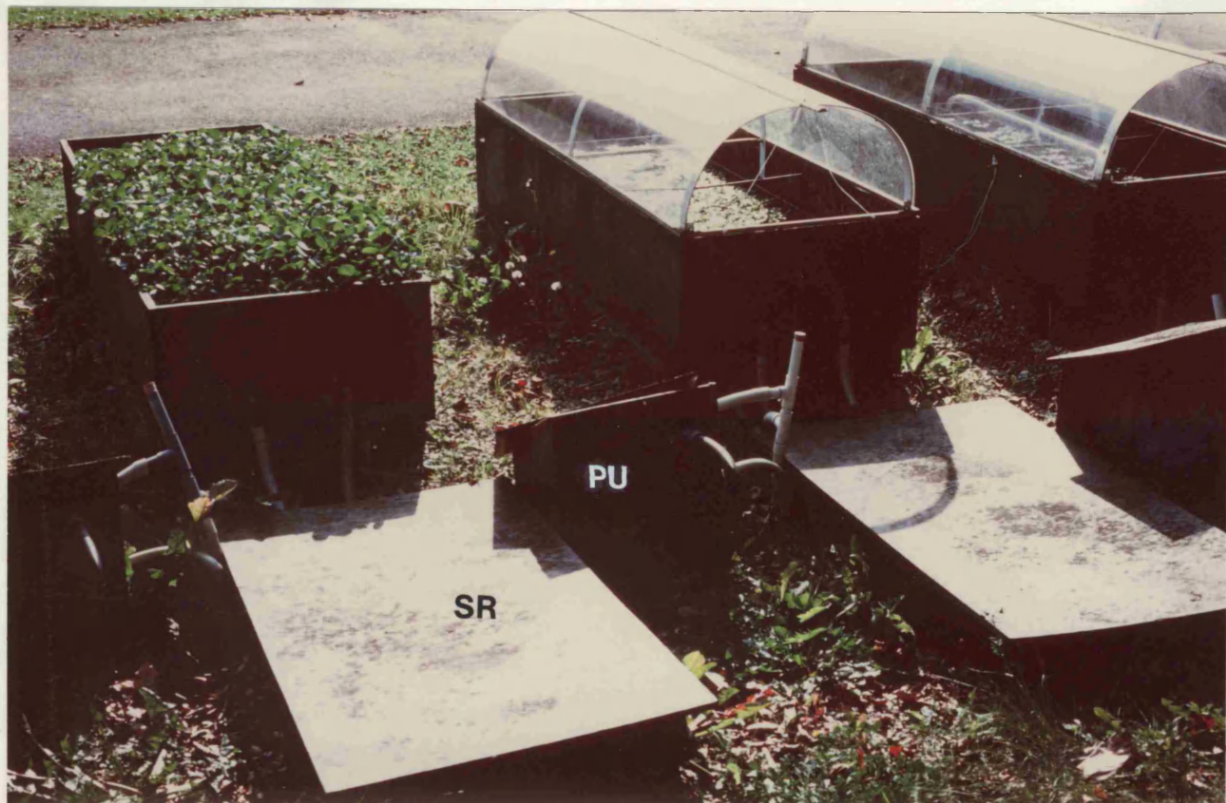
A commercially cultivated strain of green watercress, *Nasturtium officinale* R.Br., was used in all studies. Seed was obtained annually from Hampshire Watercress Ltd., Fobdown Farm, Alresford, Hampshire and stored at -10°C in a sealed jar with a sachet of silica gel. Seed viability was tested at 20°C on moist filter paper, with 90% germination.

For experimental purposes seed was sown in trays of Stockwell Brand medium-washed grit and raised under mist propagation at 20°C . Seedlings were transplanted 14 days after sowing into one of two types of watercress bed simulation tank according to the degree of environmental control required.

2.1.2 Natural Environment Simulation Tanks

Six outdoor watercress bed simulation tanks were situated at the Bath University Field Station at Claverton Down (Spence, 1980). The tanks measured $180 \times 60 \times 33$ cm high and were constructed of 19 mm marine plywood, each with a reservoir sunk into the ground giving a capacity of 350 dm^3 nutrient solution. Solutions were recirculated using a centrifugal water pump (Stuart Turner Ltd., Type 16) at $10 \text{ dm}^3 \text{ min}^{-1}$, through two inlet pipes onto a plastic tray, $55 \times 5.0 \times 2.0$ cm high, which functioned as a weir. At the opposite end of the tank a 17 cm weir separated the 14 cm deep substrate, 6 mm water-washed pea gravel, from the outlet holes giving

Plate 4. Natural Environment Simulation Tanks.



SR = solution reservoir

PU = pumping unit

an effective cropping area of 0.912 m^2 .

During the early stages of growth and also during cold weather, plants were protected using specially constructed tunnels of 20 thou. clear PVC fitted over individual tanks (Plate 4).

2.1.3 Controlled Environment Simulation Tanks

Six growth units housed in an insulated greenhouse allowed control of photoperiod and solution temperatures; air temperatures were ambient.

The growth units each consisted of a 15 mm marine plywood tank, 170 x 40 x 25 cm high, enclosed in a 3 mm hardboard cabinet, 200 x 80 x 95 cm high, supported on a Dexion frame (Spence, 1980; Rothwell, 1983). Lighting was provided by six parallel 2 m white 75 - 85 W fluorescent reflective tubes, suspended 50 cm above each tank. The cabinet was lined with reflective foil and light intensity at plant height was $c. 120 \mu\text{E m}^{-2} \text{sec}^{-1}$ PAR (400 - 700 nm). Photoperiod was controlled by time switches. Solution temperature was controlled thermostatically by a refrigeration unit through which the nutrient solution was passed. Pipes and reservoirs were lagged to minimise changes in solution temperature.

The system employed a solution of 100 dm^3 volume recirculated at $2.0 \text{ dm}^3 \text{ min}^{-1}$ by a centrifugal pump (2.1.2). A weir at the top of the tank ensured even distribution of the inlet

solution and at the outlet end a 13 cm weir led to the drainage holes.

Plate 5 shows a controlled environment growth unit.

2.1.4 Hydroponic Cultivation Method

Plants in the controlled environment tanks were grown without substrate (Rothwell, 1983) to allow accurate manipulation of the root ionic environment and accurate determination of root weights.

Black polythene was stretched over plastic seed half-trays, 21 x 15 x 5.0 cm deep, into whose sides fourteen 10 mm - diameter holes had been drilled to facilitate circulation of nutrient solution. Four lengthwise slits were cut in the polythene and the covered trays were floated in the tanks, ten trays per tank, so the underside of polythene was in contact with the irrigating solution. The trays floated naturally in this position with the upper surface of polythene dry, but a plastic mesh was placed underneath them as a safeguard against sinking.

Acid-washed sand, 40 - 100 mesh, was poured along the slits in the polythene and this drew up nutrient solution by capillary action. Ten watercress seedlings were placed on each strip of sand and quickly rooted through into solution.

2.1.5 Nutrient Solutions

Experimental solutions were made up using Bath University's

Plate 5. Controlled Environment Simulation Tank.



mains water supply. Periodic analysis (2.4) indicated that its ionic composition was consistent, providing a reliable source of basic irrigating solution.

Mineral nutrient composition of the mains supply is given in Table 1 and compared with previous analysis by Rothwell (1983). A commercial supply of watercress irrigating water from Hampshire Watercress Ltd. was also analysed.

The Ca and Mg contents of the mains water were considered adequate for watercress growth, but N P K and micronutrients were supplemented. Solutions were analysed daily for N P and K and replenished according to individual uptake.

Concentrations of all macronutrient stock solutions were $1 \times 10^5 \text{ mg dm}^{-3}$ so that addition of 1 cm^3 stock solution to 100 dm^3 irrigating solution increased its concentration by 1 mg dm^{-3} .

Compositions of macronutrient stock solutions are given in Table 2.

Trace elements were not monitored continuously but a half-strength ARC micronutrient solution was added regularly to ensure they did not become limiting to growth (Table 3). Iron was supplied as ferric EDTA.

Solutions were not buffered but pH variations were negligible due to the high buffering capacity of the CaCO_3 -rich mains water.

Table 1. Mineral composition of Bath University mains water and a commercial supply from Hampshire
Watercress Ltd., Fobdown Farm.

Source		Elements (mg dm ⁻³)								pH	k (μS)
		N	P	K	Ca	Mg	Fe	Mn	Zn		
Bath University	1980	3.75	0.01	2.5	107	8.4	0.02	0.01	0.01	7.4	
	1984	4.11	0.32	2.7	147	7.4	0.02	0.01	0.01	7.1	623
Commercial supply 1985		4.5	0.02	1.1	95	1.3	0.03	0.01	0.02	7.4	439

Table 2. Composition of macronutrient stock solutions (SS; g dm^{-3}).

Elemental concentration of all stock solutions was

$1 \times 10^5 \text{ mg dm}^{-3}$.

Element	Chemical Compound	SS (g dm^{-3})
$\text{NO}_3\text{-N}$	NaNO_3	607
$\text{NH}_4\text{-N}$	$(\text{NH}_4)_2\text{SO}_4$	472
P	$\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	503
K	KCl	191

Table 3. Composition of micronutrient stock (SS; g dm⁻³) and irrigating solutions (IS; mg dm⁻³).

Irrigating solutions contained 20 cm³ stock solution per 100 dm³ mains water.

Element	Chemical compound	SS (g dm ⁻³)	IS (mg dm ⁻³)
B	H ₃ BO ₃	1.43	0.050
Cu	CuSO ₄ ·5H ₂ O	0.10	0.005
Mn	MnSO ₄ ·4H ₂ O	2.03	0.100
Mo	(NH ₄) ₆ Mo ₇ O ₂₄ ·4H ₂ O	0.045	0.005
Zn	ZnSO ₄ ·7H ₂ O	0.55	0.025
Fe	Fe-EDTA	32.86	1.0

2.2 Plant Tissue Analysis

2.2.1 Sample Preparation

Plants were washed several times in distilled water and senescing leaves were discarded. Plants were then divided into shoot and root portions and tissue samples dried in an oven at 110°C for 24 h. Samples were then crushed using a pestle and mortar and stored in sealed polythene tubes until required. Immediately prior to analysis, sub-samples were ground to pass through a 40 mesh sieve, dried at 110°C for 1 h and cooled in a desiccator.

2.2.2 Kjeldahl Digestion for Nitrogen, Phosphorus and Potassium Determination

Duplicate samples of c. 50 mg were accurately weighed into 20 cm³ Excelo tubes. A 2 cm³ volume of selenium/sulphuric acid, 1 g Se per 200 cm³ H₂SO₄, was added to each tube and the tubes heated in an aluminium block (Cumbus, 1975). Heating was continued until the digests became clear and then for a further 1 h: total period for digestion was 4 – 6 h. After cooling, the digests were diluted to 20 cm³ with deionised water. Solutions were filtered through Whatman's No. 541 filter paper and stored in sealed polythene tubes.

2.2.3 Dry Ashing for Calcium, Magnesium, Iron, Zinc and Manganese Determination

Duplicate 0.5 g samples were weighed into 50 cm³ Jena glass conical flasks and ashed overnight at 450°C in a muffle furnace. The ash was dissolved in 1 cm³ of 3 : 1 v/v

nitric/perchloric acids and heated to dryness under a refluxing funnel. After cooling, 5 cm³ 0.5 M hydrochloric acid and 0.5 cm³ freshly prepared 0.5% w/v sodium nitrate solution were added and the mixture refluxed for a further 10 min. Cooled solutions were transferred to 10 cm³ Excelo tubes, 2 cm³ of a 500 mg dm⁻³ lanthanum chloride solution added, and diluted to 10 cm³ with deionised water. Digests were stored in sealed polythene tubes until required for analysis.

2.3 Analytical Methods

2.3.1 Flow Injection Analysis

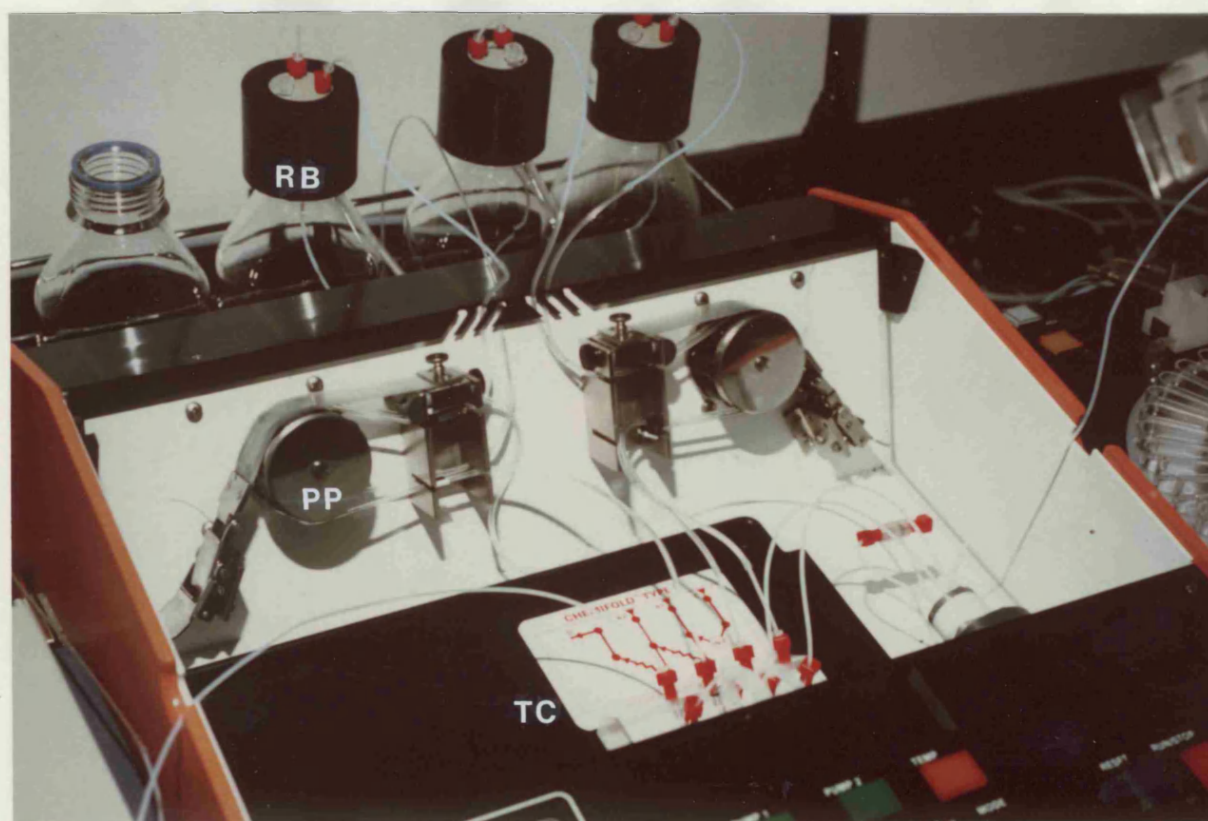
Determinations of nitrogen and phosphorus in digest solutions and aqueous samples were by Flow Injection Analysis, FIA, using a commercially available system (Tecator Ltd., Thornbury, Bristol). This comprised the flow injection analyser itself (Tecator 5020), an automatic sampler (Tecator 5007) and a printer (Alphacom 40). The detector was a Cecil 303 grating spectrophotometer connected to a chart recorder (Vitatron 2001).

Plate 6 shows the complete assembly.

Manifolds

Manifolds (Tecator Chemifolds) were made of perspex drilled in configuration according to the number of reagents involved. Reagent tubes and reaction coils were connected using screw attachments and reaction coils were selected to ensure complete

Plate 7. Flow Injection Analyser.



RB = reagent bottles

PP = peristaltic pumps

TC = Tecator Chemifolds

reagent mixing: tube id was 0.5 mm; tube lengths were multiples of 30 cm.

Each manifold was set on a tray which lay in the chamber of the flow injection analyser and reagents were pumped by two peristaltic pumps (Plate 7). Pre-calibrated pump tubes ensured accurate flow rates according to the determination being performed.

Sample injection was fully automated to inject a reproducible volume of analyte into the carrier stream. Sample volume was selected according to the determination being performed and the automatic sampler introduced each one as soon as the previous sample cleared the detector.

Detection

All determinations were based on colorimetric techniques and detection was via a flow-through cuvette (Hellma Type 178QS; volume 80 μ l; light path 10 mm) fitted in the spectrophotometer.

The chart recorder provided a continuous record of signal peaks which resulted from optical density changes in the reaction stream. Peak height was related to concentration of the analyte and this was calibrated by injecting a series of standards.

Calibration

The analyser incorporated a microprocessor which could be

programmed with the concentrations of the standards so that sample peaks were then converted directly into units of concentration. The printer provided a permanent record of concentration values.

Where the calibration curve was known to be linear the micro-processor's linear calibration mode was used; points which formed a concave curve were calibrated using the Lagrange mode. A recalibration function allowed repeated adjustment of the calibration graph.

2.3.2 Determination of Nitrogen in Kjeldahl Digests by Flow

Injection Analysis

The method was based on those described by Stewart *et al.* (1976) and Hansen *et al.* (1977) for the determination of ammonia by the Berthelot reaction. Ammonia is oxidised by hypochlorite, to chloramine, which reacts with phenol to give a blue indophenol dye. This is detected spectrophotometrically at 620 nm.

Reagents

Alkaline phenol: 50 g phenol and 120 g sodium hydroxide were dissolved in the minimum volume of deionised water. A 330 cm³ volume of ethanol was added and the solution diluted to 1 dm³ with deionised water.

Alkaline hypochlorite: 20 g sodium hydroxide and 20 g sodium

tetraborate decahydrate were dissolved in 800 cm³ of 'Chloros' bleach (c. 4% active chlorine). The solution was diluted to 1 dm³ with deionised water and filtered using Whatman No. 541 paper.

Standards

A range of nitrogen standards up to 50 mg dm⁻³ were made by dilution of a 1000 mg dm⁻³ solution of ammonium sulphate. All standards were diluted in 1 M H₂SO₄ which also provided the blank (0 mg dm⁻³ N).

Manifold

Details of the manifold are given in Figure 1.

Procedure

Sample volume was 30 µl.

Reagents were pumped at 0.32 cm³ min⁻¹.

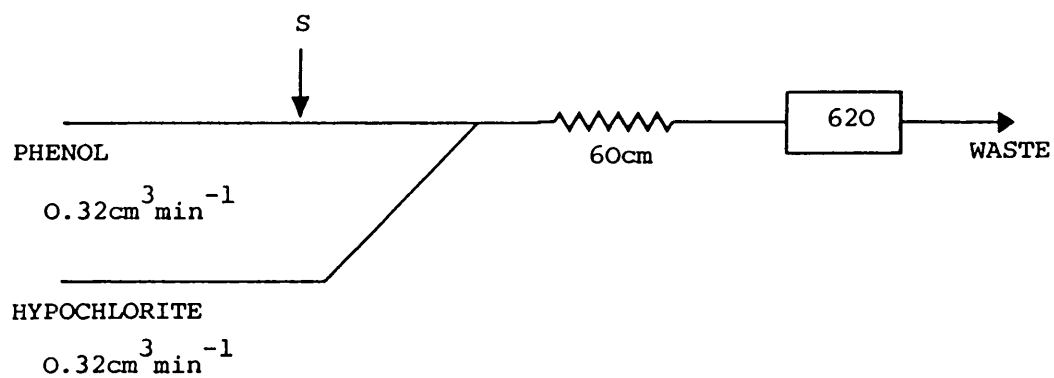
Detection was at 620 nm.

Calculation of Results

Samples were diluted 1 part digest solution to 4 parts 1 M H₂SO₄ to bring them within 0 - 50 mg dm⁻³. Dilution factors were accurately determined using known weights of plant tissue (2.2.2) and used to calculate tissue concentrations, expressed as % N DW.

Figure 1.

FIA Manifold used in the Determination of
N in Plant Digests.



Sample volume, $30\mu\text{l}$, injected at S.

Reaction coil, 60cm length.

Reagent flow rates, $0.32\text{cm}^3\text{min}^{-1}$.

Detection at 620nm.

2.3.3 Determination of Phosphorus in Kjeldahl Digests by Flow

Injection Analysis

The method was based on those described by Ruzicka and Stewart (1975) and Hansen *et al.* (1977). Phosphate reacts with molybdenum (VI) forming 12-molybdophosphoric acid which is reduced by ascorbic acid to heteropolyphosphomolybdenum blue. This is detected spectrophotometrically at 660 nm.

Reagents

Acid molybdate: 6.1793 g ammonium heptamolybdate were dissolved in 1 dm³ 0.4 M nitric acid.

Ascorbic acid: 5% w/v aqueous solution of D-iso-ascorbic acid sodium salt.

Carrier stream: 0.4 M nitric acid.

Standards

A range of phosphorus standards up to 20 mg dm⁻³ were made by appropriate dilution of a 1000 mg dm⁻³ solution of potassium dihydrogen orthophosphate.

Manifold

Details of the manifold are given in Figure 2.

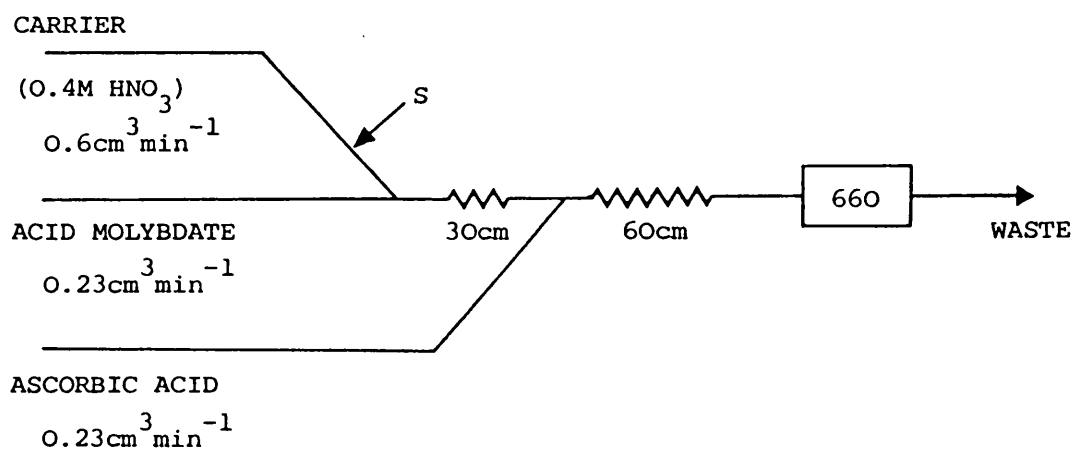
Procedure

Sample volume was 30 µl.

Reagents were pumped at 0.23 cm³ min⁻¹ and the carrier

Figure 2.

FIA Manifold used in the Determination of
P in Plant Digests.



Sample volume, $30 \mu\text{l}$, injected at S.

Reaction coils, 30cm and 60cm.

Carrier flow rate, $0.6 \text{ cm}^3 \text{ min}^{-1}$.

Reagent flow rates, $0.23 \text{ cm}^3 \text{ min}^{-1}$.

Detection at 660nm.

stream at $0.6 \text{ cm}^3 \text{ min}^{-1}$.

Detection was at 660 nm.

Calculation of Results

Samples were analysed directly without dilution and concentrations were converted into tissue concentrations expressed as % P DW.

2.3.4 Determination of Potassium in Kjeldahl Digests by Flame Photometry

An EEL flame photometer, fitted with a potassium filter, was used according to manufacturer's instructions.

Standards

A range of potassium solutions up to 100 mg dm^{-3} were made by appropriate dilution of a 1000 mg dm^{-3} solution of potassium chloride.

Calculation of Results

The standards were used to construct a calibration curve. Many samples required dilution to bring them within the $0 - 100 \text{ mg dm}^{-3}$ range and these dilution factors were taken into account when calculating % K DW.

2.3.5 Determination of Calcium, Magnesium, Iron, Zinc and Manganese in Digest Solutions by Atomic Absorption Spectrophotometry

Atomic absorption spectrophotometry (AAS) is a technique

which uses the principle that no two elements have resonance lines of the same wavelength. However, the response of one element may be suppressed by the presence of others. Phosphate, sulphate, silicate and aluminate all depress the absorbance of alkaline earth metals by forming stable compounds which have different absorbance characteristics to the free metal elements. The presence of such compounds reduces the sensitivity of AAS.

The problem is overcome by adding an excess of another element, e.g. lanthanum, which forms a stable compound with interfering anions, so releasing the metal ions. Lanthanum was added to standards and samples at a rate of 2 cm³ lanthanum chloride solution (500 mg dm⁻³) to 8 cm³ of sample.

Instrumentation

An EEL atomic absorption spectrophotometer was used in all determinations according to manufacturer's instructions.

Calculation of Results

Using an appropriate range of standards, a calibration curve was constructed for each element. Tissue concentrations were calculated and expressed in mg (kg DW)⁻¹.

2.4 Water Analysis

Conductance (k) was measured using an electric conductivity meter (Portland Electronics Ltd., model P310) fitted with

a glass/platinum electrode. Units were micro siemens (μS).

The pH of samples was determined using an electric pH meter (Pye Unicam, model 291, mk 2) fitted with a glass/calomel electrode.

Calcium, magnesium and micronutrients were determined by AAS (2.3.5).

Potassium was determined by Flame Photometry (2.3.4).

Nitrogen and phosphorus were determined using FIA.

2.4.1 Determination of Phosphate by Flow Injection Analysis

The method was based on those described by Hansen and Ruzicka (1979) and Ruzicka and Hansen (1981) and the chemistry was based on the molybdenum blue method (2.3.3). However, P concentrations in aqueous solutions were lower than in Kjeldahl digests and larger sample volumes were required.

Reagents

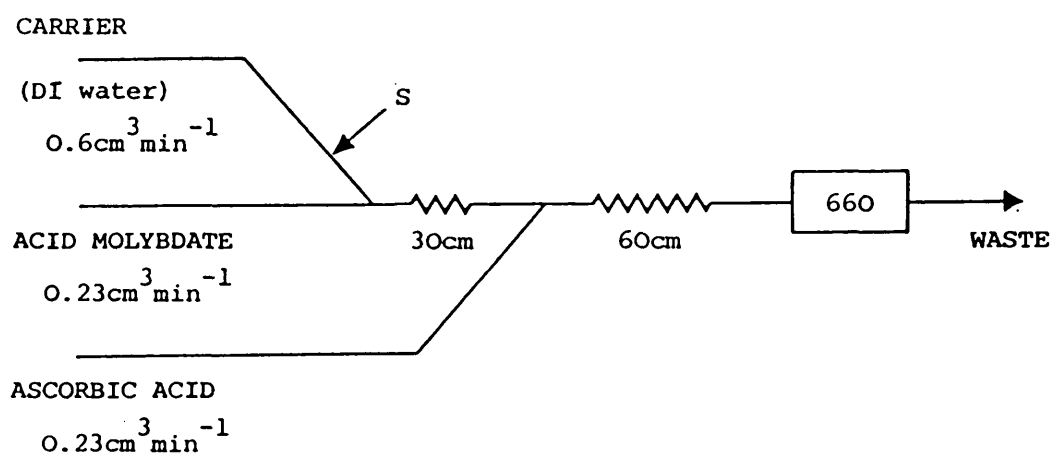
Reagents were as in 2.3.3 except for the carrier stream which, in this case, was deionised water.

Standards

A range of phosphorus standards up to 5.0 mg dm^{-3} were prepared as in 2.3.3.

Figure 3.

FIA Manifold used in the Determination of
P in Aqueous Solutions.



Sample volume, 200 μ l, injected at S.

Reaction coils, 30cm and 60cm.

Carrier flow rate, $0.6 \text{ cm}^3 \text{ min}^{-1}$.

Reagent flow rates, $0.23 \text{ cm}^3 \text{ min}^{-1}$.

Detection at 660nm.

Manifold

Details of the manifold are given in Figure 3.

Procedure

Sample volume was 200 μl .

Reagents were pumped at $0.23 \text{ cm}^3 \text{ min}^{-1}$ and the carrier at $0.6 \text{ cm}^3 \text{ min}^{-1}$.

Detection was at 660 nm.

Calculation of Results

Many samples from concentrated nutrient solutions required dilution to bring them within $0 - 5.0 \text{ mg dm}^{-3}$ but mains water and dilute nutrient solutions were analysed directly. Samples were calibrated in mg dm^{-3} using the linear calibration mode (2.3.1).

2.4.2 Determination of Nitrate by Flow Injection Analysis

The method was based on those described by Anderson (1979) and Giné *et al.* (1980). The sample is passed through a copperised cadmium column which reduces nitrate to nitrite. The nitrite reacts with sulphanilamide to form a diazo compound which is coupled with N-(1-naphthyl) ethylene diamine dihydrochloride (NNEDD) to give a purple-coloured complex. This is an azo dye which is detected spectrophotometrically at 540 nm.

Reagents

Carrier stream: 10.7 g ammonium chloride were dissolved in 1 dm³ deionised water and a drop of wetting agent added (30% Brij 35).

Colouring agent: 52 cm³ concentrated hydrochloric acid were added to 600 cm³ deionised water and 10 g sulphanilamide added. The solution was diluted to 1 dm³ with deionised water.

Complexing agent: 0.5 g NNEDD were dissolved in 500 cm³ deionised water. This reagent was made fresh each week and stored in an amber borosilicate bottle.

Copperised cadmium: Cadmium granules (30 mesh) were washed in 0.5 M hydrochloric acid and rinsed in distilled water. They were then rinsed in 1% w/v copper sulphate solution and then in carrier solution. The copperised cadmium was stable for several months if stored in carrier solution.

Standards

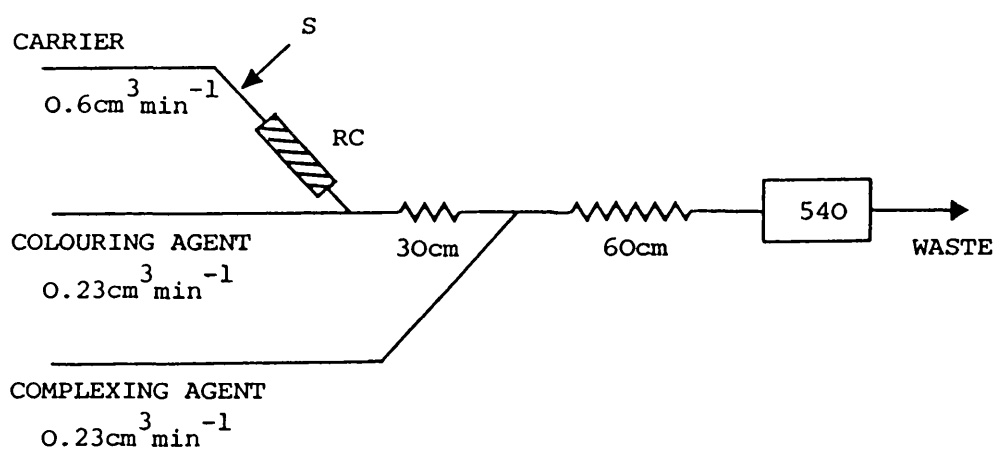
A range of nitrate standards up to 13 mg dm⁻³ were prepared by appropriate dilution of a 1000 mg dm⁻³ solution of sodium nitrate.

Manifold

The manifold is shown in Figure 4.

Figure 4.

FIA Manifold used in the Determination of
Nitrate - N in Aqueous Solutions.



RC = Reductor Column

Sample volume, 30 μ l, injected at S.

Reaction coils, 30cm and 60cm.

Carrier flow rate, 0.6 cm³ min⁻¹.

Reagent flow rates, 0.23 cm³ min⁻¹.

Detection at 540nm.

Its main feature is the incorporation of a reductor column (Tecator Reaction Column, RCO2). This was a 6 cm length of 3 mm id glass tube packed with granules of copperised cadmium. Glass wool plugs at either end prevented small particles being washed through the column into the detector. Before use, the reductor column was activated by injecting a 1000 mg dm^{-3} nitrate solution. It was then stabilised by injecting a 1.0 mg dm^{-3} nitrate solution until repeatability was obtained.

Procedure

Sample volume was 30 μl .

Reagents were pumped at $0.23 \text{ cm}^3 \text{ min}^{-1}$ and the carrier stream at $0.6 \text{ cm}^3 \text{ min}^{-1}$.

Detection was at 540 nm.

Samples passed through the reductor column gave the sum of nitrate and nitrite concentrations whilst samples by-passing the column gave concentrations of nitrite only. Nitrate concentrations were calculated by subtraction. In practice it was found that mains water and irrigating solutions contained no detectable nitrite so all values referred to nitrate nitrogen.

Calculation of Results

Many samples from concentrated nutrient solutions required dilution to bring them within $0 - 13 \text{ mg dm}^{-3}$ but mains water

and dilute nutrient solutions were analysed directly. Samples were calibrated in mg dm^{-3} using the Lagrange calibration mode (2.3.1).

2.4.3 Determination of Ammonium by Flow Injection Analysis

The method was based on that described by Mackereth (1963) using the indophenol blue method (2.3.2). This is sensitive down to 5 mg dm^{-3} ammonium in aqueous samples (Krug *et al.*, 1979) which was sufficiently accurate for the present investigation.

Reagents

These were as in 2.3.2 with a carrier stream of deionised water.

Standards

Ammonium solutions in the range $5 - 25 \text{ mg dm}^{-3}$ were made by diluting a 1000 mg dm^{-3} solution of ammonium sulphate.

Manifold

Details are given in Figure 5.

Procedure

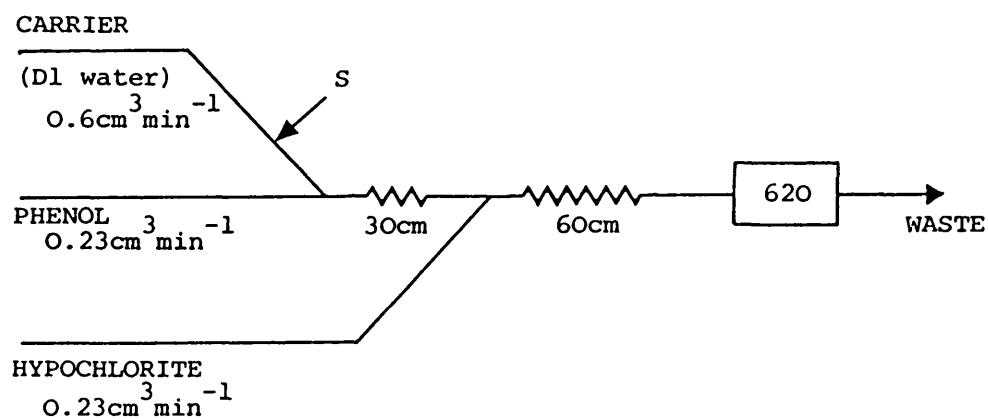
Sample volume was $30 \mu\text{l}$.

Reagents were pumped at $0.23 \text{ cm}^3 \text{ min}^{-1}$ and the carrier at $0.6 \text{ cm}^3 \text{ min}^{-1}$.

Detection was at 620 nm .

Figure 5.

FIA Manifold used in the Determination of
Ammonium - N in Aqueous Solutions.



Sample volume, 30 μl , injected at S.

Reaction coils, 30cm and 60cm.

Carrier flow rate, $0.6 \text{ cm}^3 \text{ min}^{-1}$.

Reagent flow rates, $0.23 \text{ cm}^3 \text{ min}^{-1}$.

Detection at 620nm.

Calculation of Results

Samples were analysed directly and calibrated in mg dm^{-3}

(2.3.1).

3. SECTION A

THE ENVIRONMENTAL CONTROL OF GROWTH

AND NUTRIENT UPTAKE IN WATERCRESS

3.1 Introduction

The environmental control of growth and morphology in watercress is well documented, with studies on the influence of daylength (Bleasdale, 1964; Spence, 1980; Rothwell, 1983) and temperature (Rothwell, 1983). Growth rate and watercress yield were found to be more dependent on temperature than on photoperiod (Rothwell, 1983). Light intensity has not previously been considered.

The present investigation aimed to study N P and K uptake by watercress and the effects of temperature, photoperiod and light intensity on uptake and growth. The first series of experiments looked at the interactions between temperature and photoperiod. The effects of light intensity were studied in a separate experiment.

3.2 The Effects of Temperature, Photoperiod and their Interactions on Uptake of N P and K

3.2.1 Materials and Methods

Plant Material

Watercress was raised from seed and plants grown at 12 h daylength and 10°C in the controlled environment tanks (2.1.3). When they had grown to 12 cm tall, uniform plants were selected and transferred to experimental conditions.

Dark Cabinets

Three cabinets of heavy gauge black polythene supported on rigid frames were constructed in the laboratory. Each cabinet

contained a waterbath in which were suspended six beakers containing nutrient solution. Baths were adjusted to maintain solution temperatures at constant 5°, 10° and 15°C. Air temperatures were 9°, 14° and 19° respectively.

Illumination was provided by four parallel 1.0 m 20 W white fluorescent tubes suspended 40 cm above the solutions, giving a light intensity at plant level of $30 \mu\text{Em}^{-2}\text{sec}^{-1}$ PAR. Time switches were used to vary photoperiod and three regimes were studied (8 h, 12 h and 16 h PP).

Environmental Regimes

Interactions between the three temperature and three photoperiodic regimes gave a total of nine treatments.

Treatments consisted of five plants, each supported in a beaker containing 500 cm^3 of nutrient solution (Table 4) and a control beaker of solution only.

Solutions were distilled water-based and, although they were unbuffered, pH remained constant at 6.7 ± 0.1 . Stirring was achieved by aeration and petri dishes were placed on top of the beakers to minimise evaporative losses.

Experiments were replicated twice giving a total of ten plants per treatment.

Procedure

Plants were acclimated to their respective temperature and photoperiodic regimes for 3 days, during which the nutrient solution was renewed at 24 h intervals. Acclimation was

Table 4. Nutrient solution used to study the environmental control

of growth and nutrient uptake.

Composition of stock (SS; g dm^{-3}) and irrigating solutions (IS; mg dm^{-3}).

Irrigating solutions contained 2.0 cm^3 stock solution per dm^3 distilled water.

Element	Chemical Compound	SS (g dm^{-3})	IS (mg dm^{-3})
N	NaNO_3	30.35	10.0
P	$\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	12.59	5.0
K	KCl	4.675	5.0
Ca	$\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$	18.33	10.0
Mg	$\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$	8.36	2.0
B	H_3BO_3	0.0286	0.010
Cu	$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$	0.0020	0.001
Mn	$\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$	0.0406	0.020
Mo	$(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$	0.0009	0.001
Zn	$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	0.0110	0.005
Fe	Fe-EDTA	3.286	1.0

immediately followed by the 5 day experimental period and solutions were not renewed during this time.

A 3.0 cm³ sample was taken from each beaker at the start of the experiment and stored in a refrigerator at 4°C. A further sample was taken on Day 5 for measurement of N P and K depletion. All samples were analysed on Day 5 using FIA to determine N (2.4.2) and P (2.4.1) and flame photometry to determine K levels (2.4).

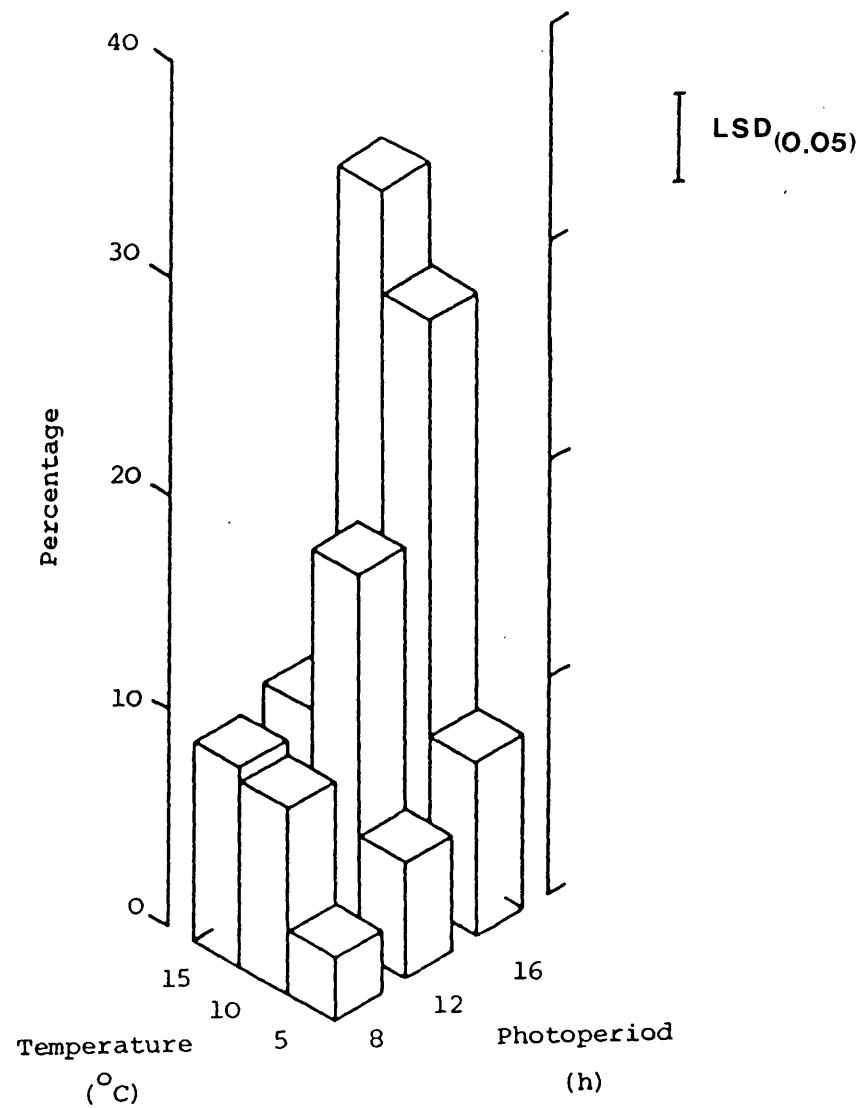
Fresh weights were recorded at the start of the experiment and at harvest. Plants were then rinsed several times with distilled water to remove any surface contamination of nutrients, and divided into shoot and root portions. These were dried in an oven at 110°C for 24 h and dry weights determined on Day 6. Micro-Kjeldahl digestion (2.2.2) was used to prepare tissue samples for mineral analysis. K was determined by flame photometry (2.3.4) and FIA used to determine N (2.3.2) and P (2.3.3).

3.2.2 Results and Discussion

Increases in fresh weight as a percentage of initial fresh weight (Figure 6) indicate the effects of temperature and daylength on growth during the 5 day period of measurement.

At constant 5° and 10°C, growth increased steadily with increasing PP.

Figure 6. The Effects of Temperature and Photoperiod on Watercress Growth.
Increase in Plant Fresh Weight as a Percentage of Initial Fresh Weight.



At constant 15°C, increasing the photoperiod from 8 h to 12 h gave little increase in growth, but a larger increase was observed when photoperiod was increased to 16 h.

At constant PP, an increase in temperature from 5° to 10°C gave a significant increase in growth. The temperature increase from 10° to 15°C gave a slight growth increase at 8 h and 16 h PP but had a depressing effect on growth at 12 h.

The effect of ^{a 5° change in} temperature is seen to depend on temperature, and a similar response has been demonstrated in many other species (Cooper, 1973).

The findings of the present investigation agree with those of Rothwell (1983) who found that reducing the temperature from a 25° day/20° night regime to a 15°/10°C regime gave a two-fold increase in the fresh weight of watercress. Other workers have also reported negative correlation between plant weight and temperature regime: Went (1957) observed increased yields of potato and tomato plants when grown under cooler conditions; Dale (1964) found negative correlation between temperature regime and plant weight of *Phaseolus vulgaris* and Thomas and Raper (1978) demonstrated an increase in weight of soyabean plants when grown under cooler conditions.

Commercial watercress is grown in beds irrigated with water whose emergent temperature is 10.5°C (1.2) and this may have had a selective effect towards a crop physiologically adapted to growth at c. 10.5°C. Such adaptation has been reported in several other species by Zhurbitzky and Shtrausberg

(1958) and Warriner *et al.* (1981).

In the present investigation the adaptation is seen to be dependent on photoperiod: at 12 h PP the optimum temperature was 10°C but at 16 h, growth was maximum at 15°C. This reflects seasonal differences in cultural management; water flow rates are slowed down in Summer allowing the water to warm up as it passes down the bed.

Dry weight as a percentage of final fresh weight is shown in Figure 7.

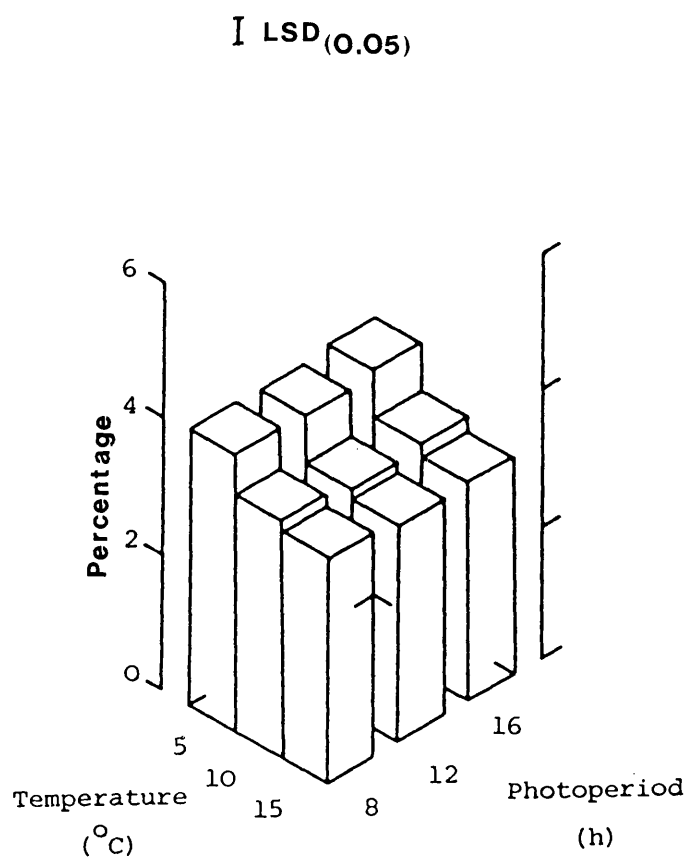
Increasing photoperiod had no effect on dry matter percentages, but there was a strong temperature dependence. Again, the temperature response was a function of temperature with the step from 5° to 10°C having a greater effect than the step from 10° to 15°C.

Increasing temperature gave a decrease in values, which agrees with observations on corn (Beauchamp and Lathwell, 1967) and birch seedlings (Ingestad, 1979), that dry matter percentages increased with decreasing temperature. The effects of low temperatures were attributed to disturbed water balance by Ingestad, who found that temperature had no effect on the nutrient status of birch seedlings.

Figure 8 shows watercress tissue concentrations of N P and K.

Nitrogen status (Fig. 8a) showed some correlation with growth and was highest at the higher temperatures and longer photoperiods.

Figure 7. Watercress Dry Weight as a Percentage of Final Fresh Weight, in relation to Temperature and Photoperiod.



N.B. Note the reversed temperature axis.

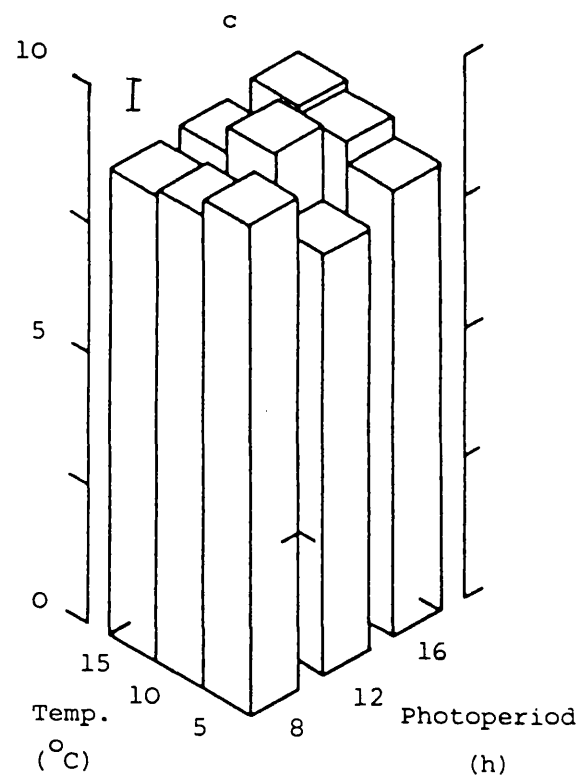
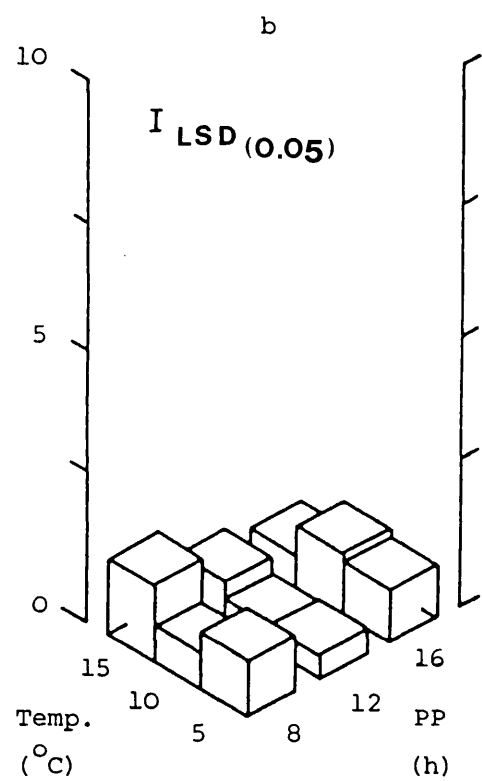
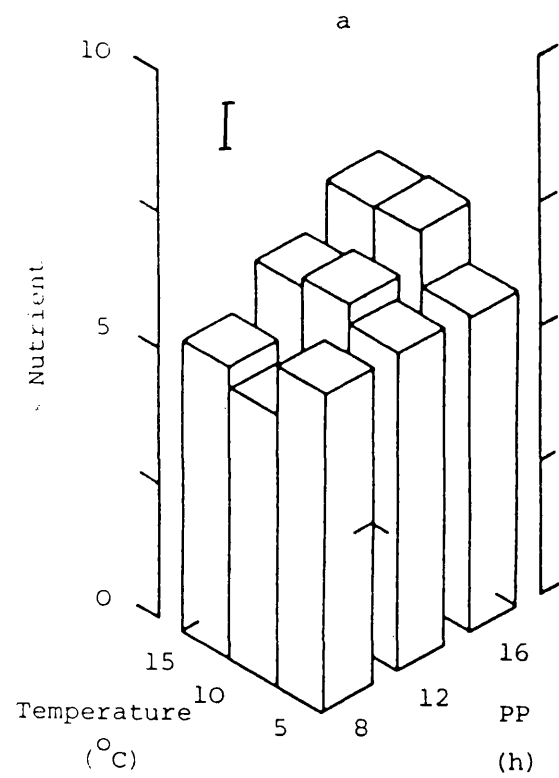
Figure 8.

Tissue Nutrient Status in Relation to
Temperature and Photoperiod

(a) Nitrogen

(b) Phosphorus

(c) Potassium.



Temperature and photoperiod had no effect on % P in watercress (Fig. 8b), although %P has shown positive correlation with temperature in alfalfa (Levesque and Ketcheson, 1963). Potassium content (Fig. 8c) was independent of temperature and photoperiod, which agrees with the observation by Williams (1961) that temperature had no effect on % K in barley. All the observed values were above the critical levels (1.3) established for watercress leaf tissue by Robinson and Cumbus (1977), and of the same order as the shoot mineral levels (1.3) recorded by Rothwell (1983).

Nutrient uptake was calculated on a dry weight basis ($\mu\text{g}(\text{gDW})^{-1}$) and results are shown in Figure 9. Nitrate uptake (Fig. 9a) was positively correlated with both temperature and photoperiod, although at 16 h PP an increase in temperature from 10° to 15°C gave a decrease in uptake. Earlier studies have reported that nitrate uptake was inhibited at low temperatures (Zhurbitzky and Shtrausberg, 1958; Gukova, 1962; Williams and Vlamis, 1962) and that the effect of temperature was greater at lower than at higher temperatures (Honert and Hooymans, 1955; Cooper, 1973). More recently, studies on tomato (Adams and Winsor, 1978) and cucumber (Adams, 1980) have shown nitrate uptake to be more dependent on light intensity than on temperature.

Absorption of P (Fig. 9b) was of a low order of magnitude compared to N and K and treatment differences were corres-

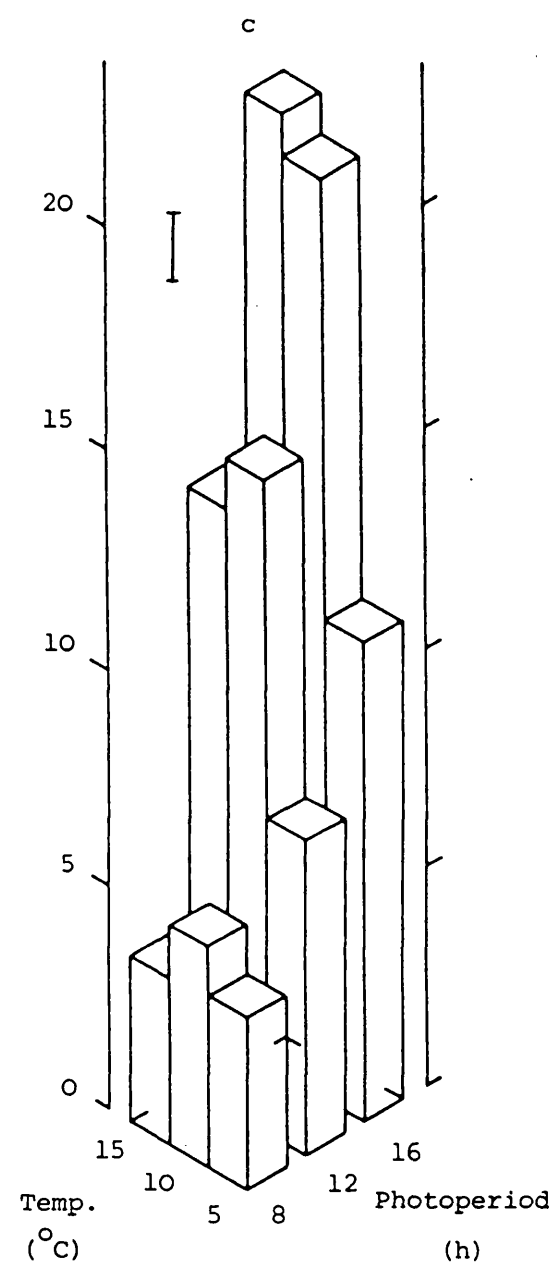
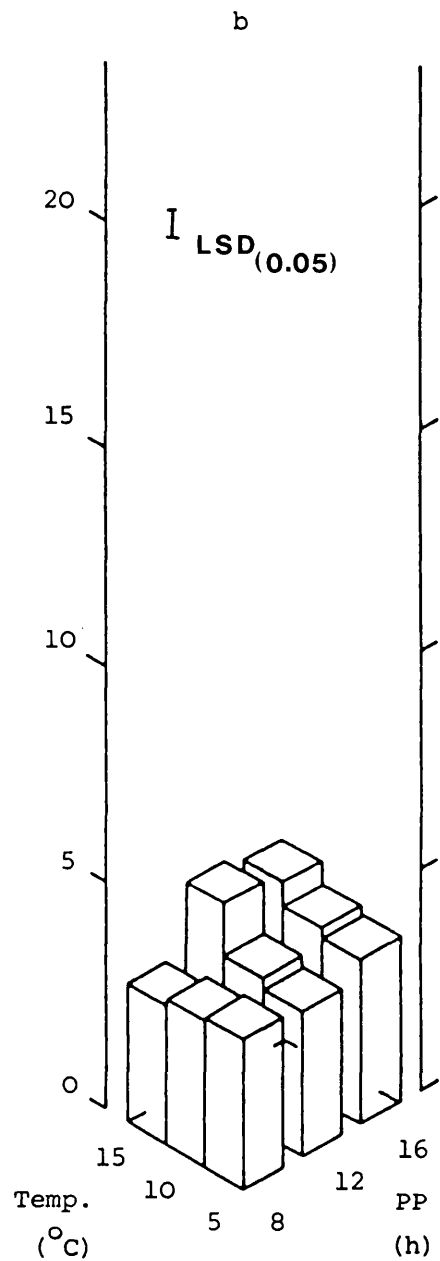
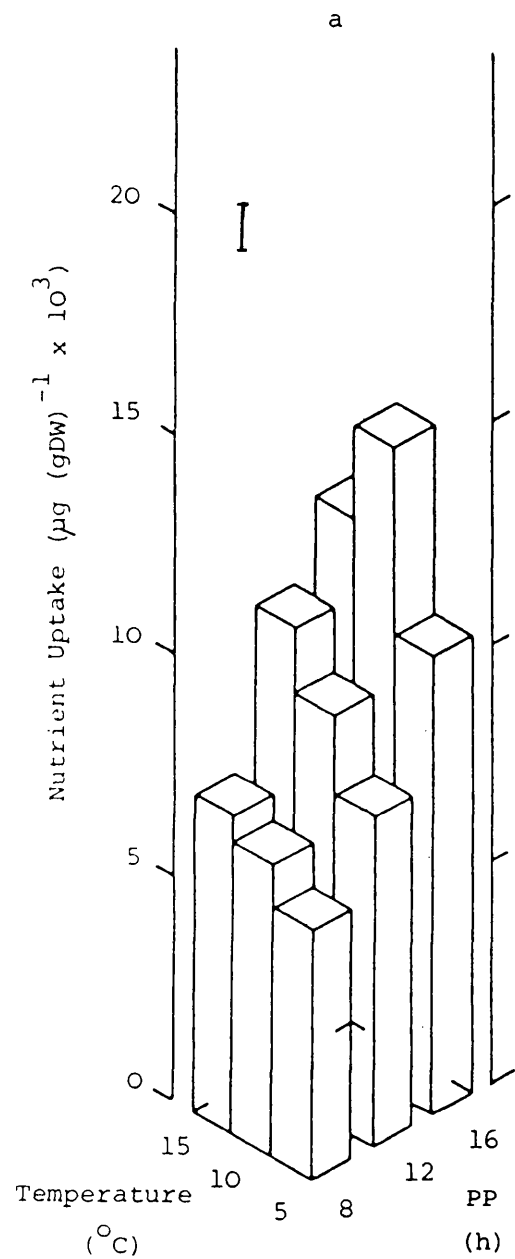
Figure 9.

Nutrient Uptake ($\mu\text{g (gDW)}^{-1}$) in relation to
Temperature and Photoperiod

(a) Nitrogen

(b) Phosphorus

(c) Potassium.



pondingly small.

At constant 8 h PP, P uptake decreased slightly as temperature increased but, at constant 12 h and 16 h PP, uptake increased with increasing temperature. The 5° increase from 10° to 15°C gave a larger increase in P absorption than the corresponding increase from 5° to 10°C.

At constant temperature, increasing photoperiod gave small increases in uptake.

Phosphate absorption was more sensitive to increasing temperature at constant photoperiod, than *vice versa* and this agrees with observations on tomato (Adams and Winsor, 1978) and cucumber (Adams, 1980). Other workers have also noted that P was absorbed more slowly at low than at high temperatures (Zhurbitzky and Shtrausberg, 1958; Gukova, 1962). Tobacco has shown an increase in P uptake when grown at increasing temperatures (McEvoy, 1960) and similar observations have been reported on *Elodea densa* (Jeschke and Simonis, 1965). The effects of low root temperatures on P nutrition have been reviewed by Sutton (1969).

In the present investigation, response to temperature was also photoperiod dependent and was not observed at 8 h PP. It is possible that a threshold photoperiod exists, below which there is no effect of temperature on P uptake. Such a threshold would also account for the observation that K uptake was insensitive to temperature at constant 8 h PP (Fig. 9c).

Comparison of Figures 6 and 9b agrees with the findings of Power *et al.* (1963) that, at low temperature, barley growth was restricted more than P uptake.

Potassium uptake (Fig. 9c) was strongly correlated with growth (Fig. 6) and this may be attributed to the role of K in plant osmotic regulation (Sutcliffe and Baker, 1981).

Potassium uptake in tomato was found to increase with increasing plant growth (Adams and Winsor, 1978) and in cucumber, K uptake increased with increasing temperature and light intensity (Adams, 1980).

In the present investigation, K absorption was positively correlated with increasing photoperiod and temperature (Fig. 9c).

At constant temperature, K uptake increased steadily with increasing PP.

At constant 8 h PP, increasing temperature had little effect on uptake. At constant 12 h and 16 h, an increase in temperature from 5° to 10°C gave a large increase in uptake but the increase from 10° to 15°C had less effect. The effects of temperature were photoperiod dependent and a threshold mechanism, as proposed for P uptake, could account for this dependence.

At 16 h PP there was no further increase in uptake when temperature was increased above 10°C and some other factor

may have become limiting to uptake at this point.

Potassium levels were not sufficiently depleted during the experiment as to become limiting (Section B: 4.3). However, the low light intensity ($30 \mu\text{Em}^{-2}\text{sec}^{-1}$ PAR) may have limited uptake and growth (3.3.2).

3.3 The Effects of Light Intensity on Uptake of N P and K

3.3.1 Materials and Methods

Plant Material

Watercress was raised from seed and grown in the controlled environment tanks (2.1.3) at 12 h daylength and 10°C. Plants were transferred to experimental conditions when 12 cm tall. For the purposes of this investigation, 40 plants in a seed half tray (2.1.4) were used in each treatment, which was replicated once.

Experimental Growth Tanks

Five polythene tanks (44 x 22 x 23 cm high) were placed in a 3 mm hardboard cabinet (200 x 80 x 95 cm high) in an insulated greenhouse at Claverton Down (2.1.3). Each tank contained 5 dm^3 of nutrient solution (Table 4) stirred by aeration. Temperatures were ambient (solution, 14°C; air, 16°C). Photoperiod was 12 h with lighting provided by six parallel 2 m white 75 – 85 W fluorescent reflective tubes suspended 50 cm above plant level, giving a light intensity of $120 \mu\text{Em}^{-2}\text{sec}^{-1}$ PAR.

Light Intensity Regimes

Experimental treatments were achieved by covering the tanks with screens of neutral density studio filter (500/03-Kodak) to give incident light intensities of 100%, 50%, 25% and 12.5% . These corresponded to values of 120, 60, 30 and 15 $\mu\text{Em}^{-2}\text{sec}^{-1}$ PAR respectively. The control tank received a light intensity of 120 $\mu\text{Em}^{-2}\text{sec}^{-1}$ PAR. Each of the four treatment tanks held 40 plants in 5 dm³ nutrient solution.

Procedure

Plants received a 3 day nutritional acclimation period at 120 $\mu\text{Em}^{-2}\text{sec}^{-1}$ PAR with the solution renewed every 24 h. Acclimation was immediately followed by the 5 day experimental period and solutions were not renewed during this time. Procedures for solution sampling, mineral analysis and fresh and dry weight measurement are described in 3.2.1.

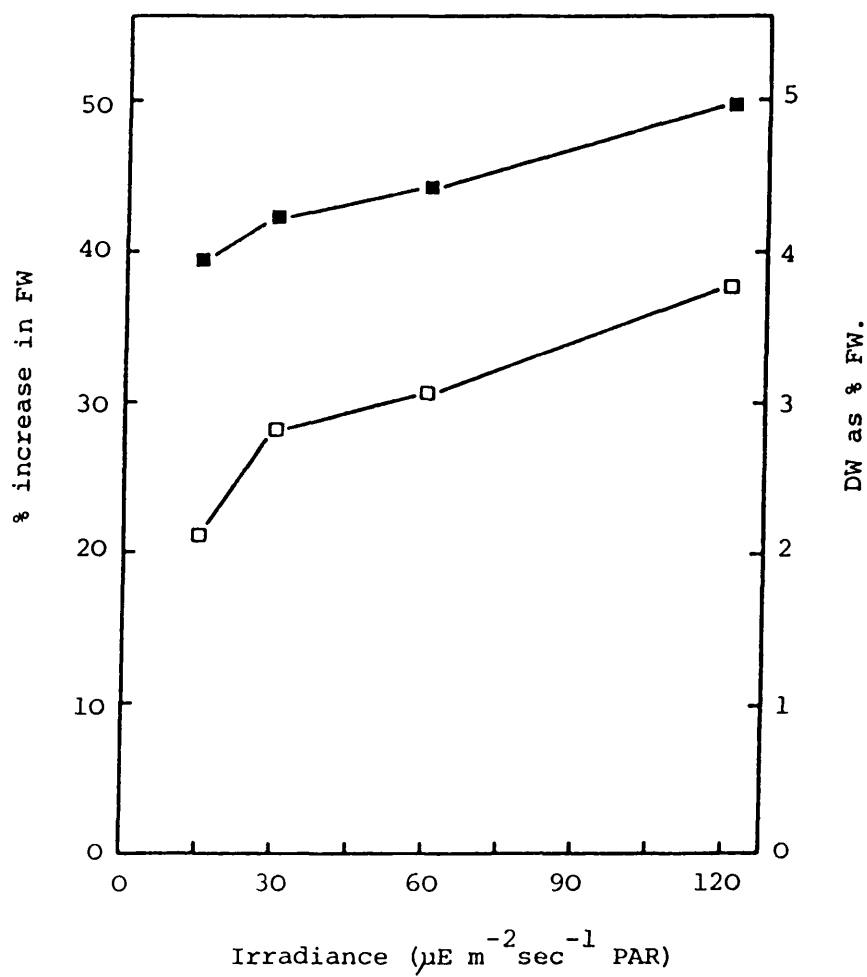
3.3.2 Results and Discussion

Percentage increases in plant fresh weight (Fig. 10) indicate the amount of growth over the 5 day experimental period. In the range studied, positive correlation was observed between light intensity and growth. A similar relationship has also been observed in alfalfa seedlings (Matches *et al.*, 1962) and in several aquatic species rooted in a river (Peltier and Welch, 1969). Other workers have reported that growth increased with increasing light intensity up to an optimum value, where the response levelled out (Cloern, 1977).

Figure 10. The effects of Light Intensity on Watercress Growth.

Fresh Weight Increase as a Percentage of Initial
Fresh Weight (\square).

Dry Weight as a Percentage of Final Fresh Weight (\blacksquare).



In the present investigation light intensity was about equivalent to that occurring outdoors on a dull day and, at such levels, the growth response was unlikely to have been saturated.

Dry weight as a percentage of final fresh weight is also shown in Figure 10. Values increased with increasing light intensity indicating an effect on plant water balance. This has also been observed in tomato (Adams and Winsor, 1978) and cucumber (Adams, 1980) where water uptake was a function of light intensity.

Figure 11 shows watercress tissue concentrations of N P and K.

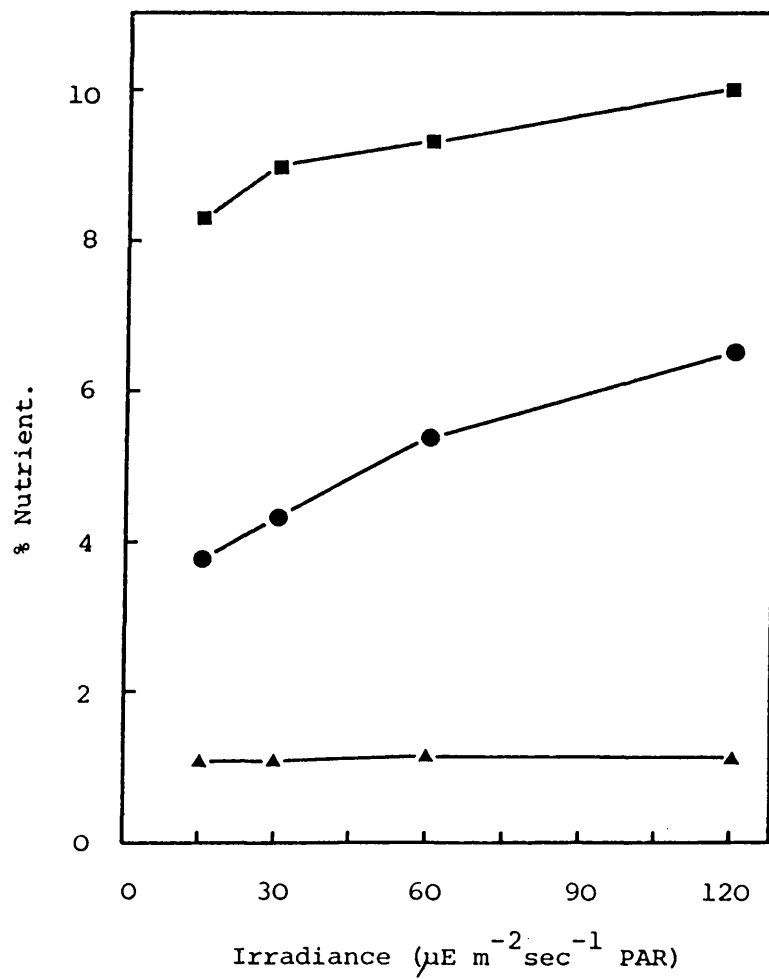
Phosphate content was independent of light intensity in the range studied.

Nitrogen and potassium contents showed positive correlation with light intensity and % K was also closely correlated with plant growth (Fig. 10).

Values for % P and % K were above the established critical concentrations (1.3) at all times; N status was below critical level except at the highest light intensity. However, critical concentrations are affected by the environment (Bates, 1971), and Ulrich (1943) found that plant nutrient status was a function of climate.

In the present investigation, shoot nutrient levels were comparable with those (1.3) obtained by Rothwell (1983).

Figure 11. Percentage N (●), P (▲) and K (■) in Watercress Dry Matter, in relation to Light Intensity.



Nutrient uptake was calculated on a dry weight basis ($\mu\text{g}(\text{gDW})^{-1}$) and results are shown in Figure 12.

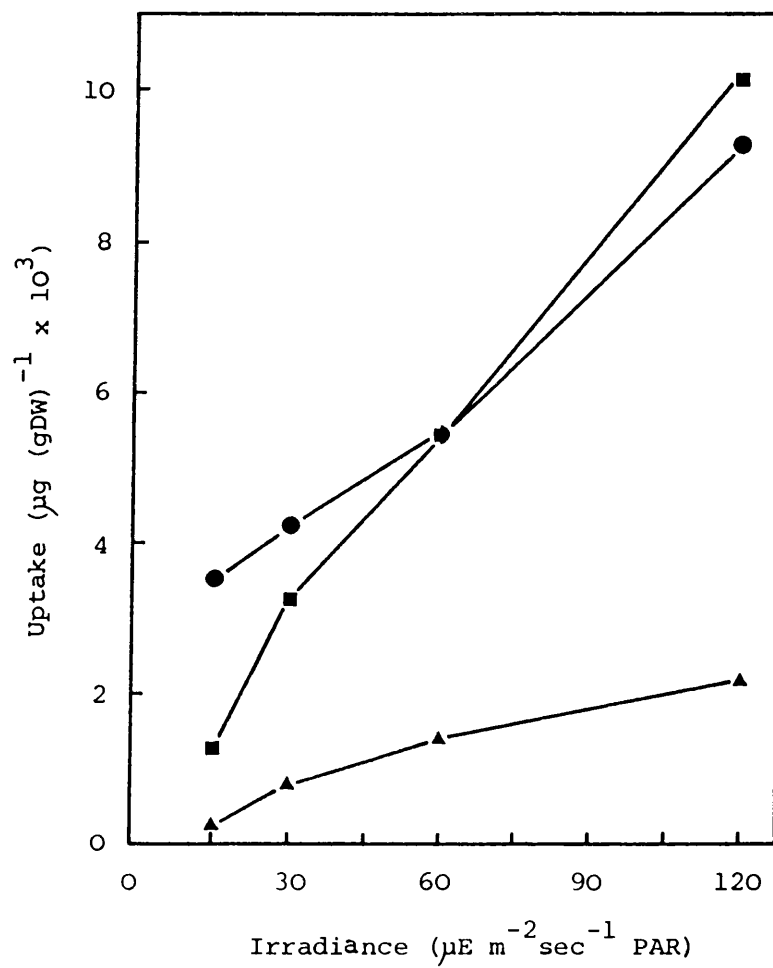
Uptake of all three elements was positively correlated with light intensity and this observation is supported by the findings of other workers. Nitrate uptake in perennial ryegrass was closely correlated with solar radiation (Clement *et al.*, 1974) and this has been reported in many other species (Barker and Mills, 1980). In tomato (Adams and Winsor, 1978) and cucumber (Adams, 1980), uptakes of N K and, to a lesser extent, P, were related to light intensity although P uptake was more dependent on temperature. Other workers have related P absorption to light intensity in eelgrass (McRoy and Barsdate, 1970) and in *Elodea densa* (Jeschke and Simonis, 1965), where the response was a function of solution concentration of P.

The effect of light on nutrient uptake is related to the supply of energy for uptake, which is saturated at a much lower light intensity than is photosynthesis (Rains, 1968). In the present investigation increasing light intensity had a greater effect on uptake, especially of N and K, than on plant growth (Fig. 10).

3.4 Summary and Conclusions

The results indicate the extent to which temperature and light, in terms of photoperiod and intensity, influence growth and nutrient uptake in watercress. Uptake has been

Figure 12. Uptake ($\mu\text{g (gDW)}^{-1}$) of N (\bullet), P (\blacktriangle) and K (\blacksquare) in relation to Light Intensity.



associated with growth in many previous environmental investigations (Zhurbitzky and Shtrausberg, 1958; Grobbelaar, 1963; Reisenauer, 1969; Ibrahim *et al.*, 1981) and results of the present investigation agree with their findings.

Doubts have been expressed (Dale, 1964) as to how far the effects of temperature could profitably be studied in isolation from light intensity and photoperiod, but few workers have studied such interactions.

The results of the present investigation indicate that interactions between temperature and photoperiod and their effects on growth and nutrient uptake are complex. The effects of temperature were dependent both on temperature and photoperiod.

Under natural environmental conditions, temperature and photoperiod vary seasonally. Treatment differences therefore represented a seasonal profile in watercress growth and nutrient uptake which has long been recognised by growers.

The Winter uptake rates of N P and K were observed by Rothwell (1983) to be c.one tenth of those in Summer.

Results of the second experiment (3.3) showed that light intensity was also a strong factor in controlling watercress growth and nutrient uptake.

Light intensity is a function of the weather and varies greatly from day to day. In this way it can modify the seasonal trends in growth and nutrient uptake to an extent not

previously recognised. Growers need to be aware of these environmental influences and to adjust the supply of water and nutrients according to daily weather and seasonal conditions.

4. SECTION B

THE SELF-REGULATION OF GROWTH

AND NUTRIENT UPTAKE IN WATERCRESS

4.1 Introduction

This series of investigations aimed to examine the intrinsic properties of watercress, with respect to its growth and nutrient uptake.

Two aspects of the control of growth and uptake have been identified and two different approaches were needed to investigate them.

The first approach (4.2) was to characterise the relationship between plant size and time, and to quantify nutrient uptake and tissue nutrient status according to stage of growth.

The second approach (4.3) was to examine the intrinsic rate of nutrient uptake by watercress, as a function of solution concentration. This would also identify the concentration below which uptake ceases, and was achieved by monitoring nutrient depletion from a recirculating solution.

4.2 Characterisation of Growth and Nutrient Uptake in Watercress according to Stage of Plant Growth

It has long been recognised that nutrient uptake increases as growth of watercress progresses (Marcel and Barbier, 1939) and this is reflected in the commercial practice of adjusting water flow rate according to stage of growth (1.2). However, no quantitative data exists concerning nutrient uptake and stage of growth, so it was decided to investigate this relationship. It was also intended

to determine the relationship between nutrient status and age of watercress tissue, as recommended by Cumbus (1975).

A dilute nutrient solution was chosen for the experiment, with levels of N P and K corresponding to those in a 5% Hoagland's solution (Hoagland and Arnon, 1950). Levels of N and P were similar to those found in commercial watercress irrigating waters, although K levels were higher than those usually observed. Commercial irrigating water may, however, contain levels of K sub-optimal for maximum growth (Rothwell, 1983) but the ratio of nutrients in Hoagland's solution has given satisfactory growth of many species (Hoagland and Arnon, 1950).

4.2.1 Materials and Methods

Plant Material

Watercress seed was germinated under mist (2.1.1) and, 14 days after sowing, transplanted into the natural environment tanks (2.1.2). Planting density was *c.* 2400 plants tank⁻¹, giving an effective density of 2630 plants m⁻².

Nutrient Regime

The irrigating solution was made by supplementing mains water with N P and K stock solutions (Table 2) to levels corresponding to 5% Hoagland's solution (Hoagland and Arnon, 1950).

Details of the solution are given in Table 5.

Table 5. Nutrient solution used to characterise growth and nutrient uptake according to plant age.

N P and K stock solutions were as in Table 2.

Micronutrients were as in Table 3.

Elements (mg dm^{-3})						pH	k(μS)
N	P	K	Ca	Mg	Fe		
10.7	1.5	11.7	147.0	7.4	1.0	8.3	800

Procedure

Solutions were sampled daily and analysed for N P and K, which were replenished according to individual uptake. Micronutrients were replenished regularly as in 2.1.5. Solutions were unbuffered, but pH remained constant throughout the experiment at 8.3 ± 0.1 . Conductance remained constant at c. 800 μ S.

The experiment ran during May - June 1985, with three replicates.

Two tanks were used to obtain quantitative data concerning nutrient uptake, and a third to obtain weekly plant samples for measurement of shoot fresh weight: because the experiment was conducted in gravel beds, it was not practicable to recover the roots.

Shoots were dried at 110°C for 24 h to give dry weight data, then tissue samples were prepared for mineral analysis by micro-Kjeldahl digestion (2.2.2). FIA was used to determine N (2.3.2) and P (2.3.3) and K was determined by flame photometry (2.3.4).

4.2.2 Results and Discussion

Growth remained vegetative throughout the 7-week period of study and plants showed no initiation of flowering during this time.

Watercress is a long-day flowering species (Bleasdale, 1964) and the major problem facing commercial cultivation

in Summer months is unwanted flowering (Stevens, 1974).

This may, however, be a stress response triggered by sub-optimal nutrient supply (Bidwell, 1979), which can be prevented by adequate nutrition.

The findings of the present investigation agree with those of Coïc *et al.* (1972), who also prevented flowering in watercress by providing plentiful nutrition.

The crop growth curve was described by plotting shoot fresh weight against time (Fig. 13).

Growth appeared to be exponential, and this was verified by taking logarithmic values of shoot fresh weight, which were also plotted against time (Fig. 14). The \log_{10} FW/time relationship gave a straight line, showing exponential growth under non-limiting conditions (Evans, 1972; Harper, 1977).

Dry weight as a percentage of fresh weight (Fig. 15) decreased as growth progressed.

In the present investigation, dry weight of mature watercress was 4.26% of fresh weight, compared to 6.7% recorded for a commercially-grown crop (Crisp, 1970). Less favourable growing conditions would account for the less succulent crop obtained commercially, and this may have been a function of environment (Section A) or nutrient supply (Rothwell, 1983).

Figure 13.

Shoot Fresh Weight as a function
of Plant Age.

Figure 14.

Shoot Fresh Weight as a function
of Plant Age :
logarithmic relationship.

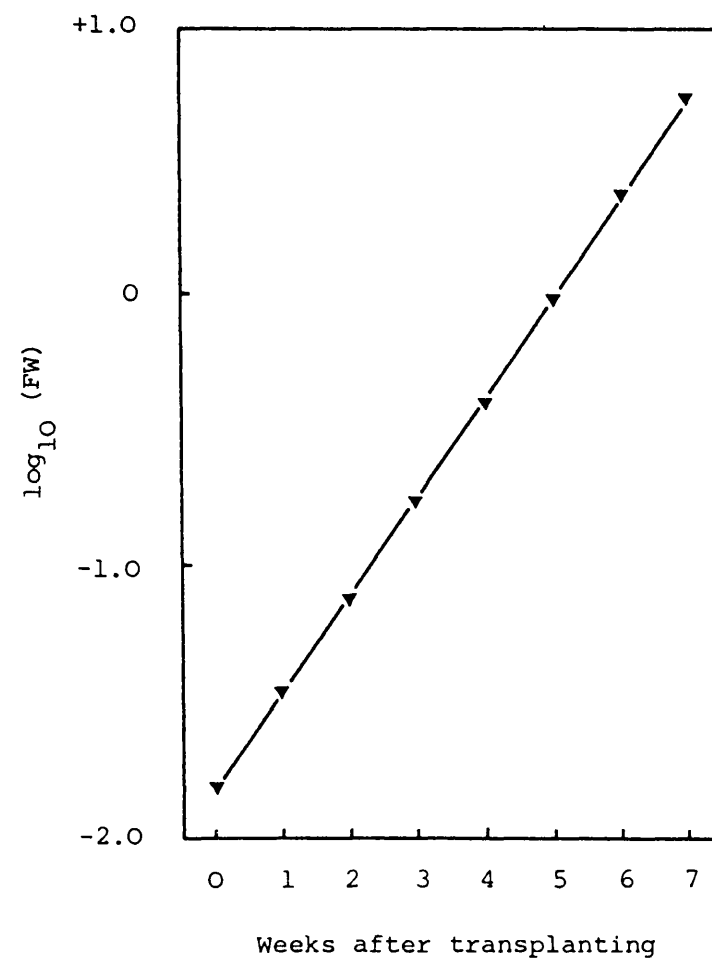
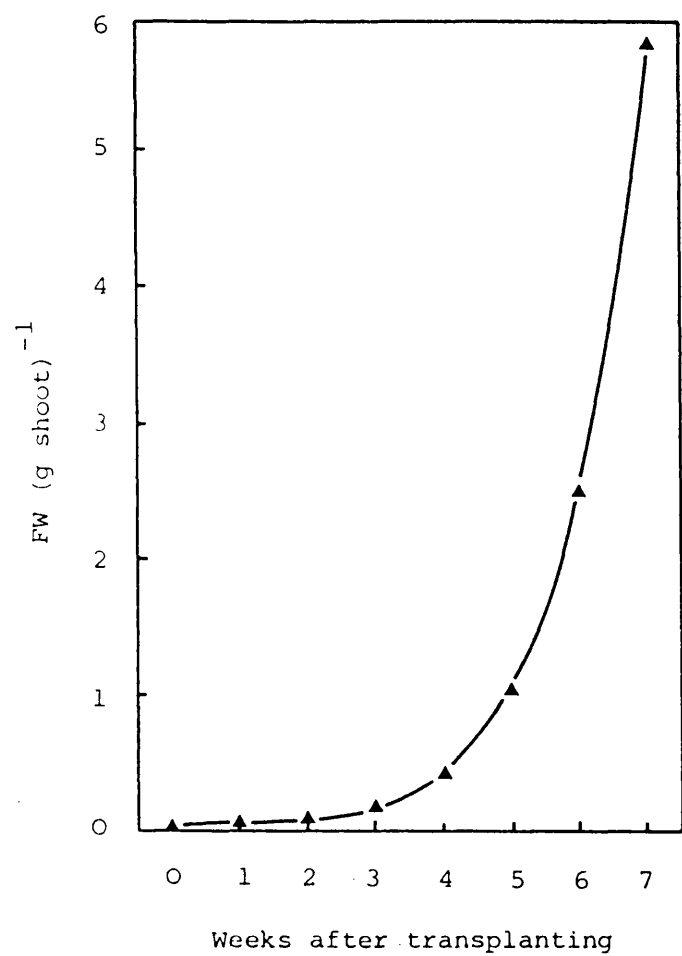


Figure 15. Watercress Dry Weight as a Percentage of Fresh Weight in relation to Plant Age.

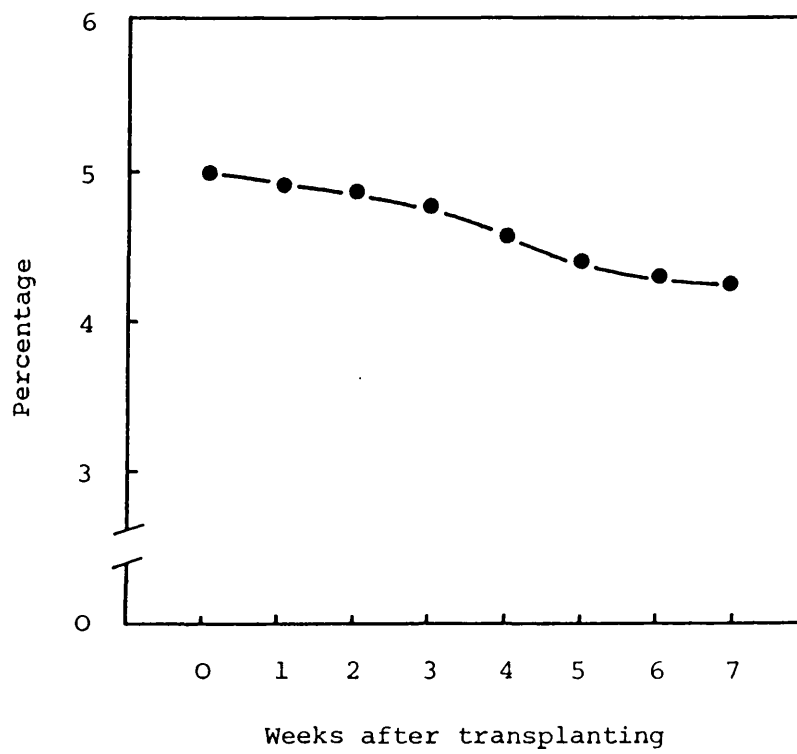


Figure 16 shows watercress tissue concentrations of N P and K as a function of stage of growth.

Concentrations of N and K increased greatly during the first week after transplanting, and continued to increase as growth progressed. Percent P was of a lower order of magnitude, but values increased steadily over the period of investigation.

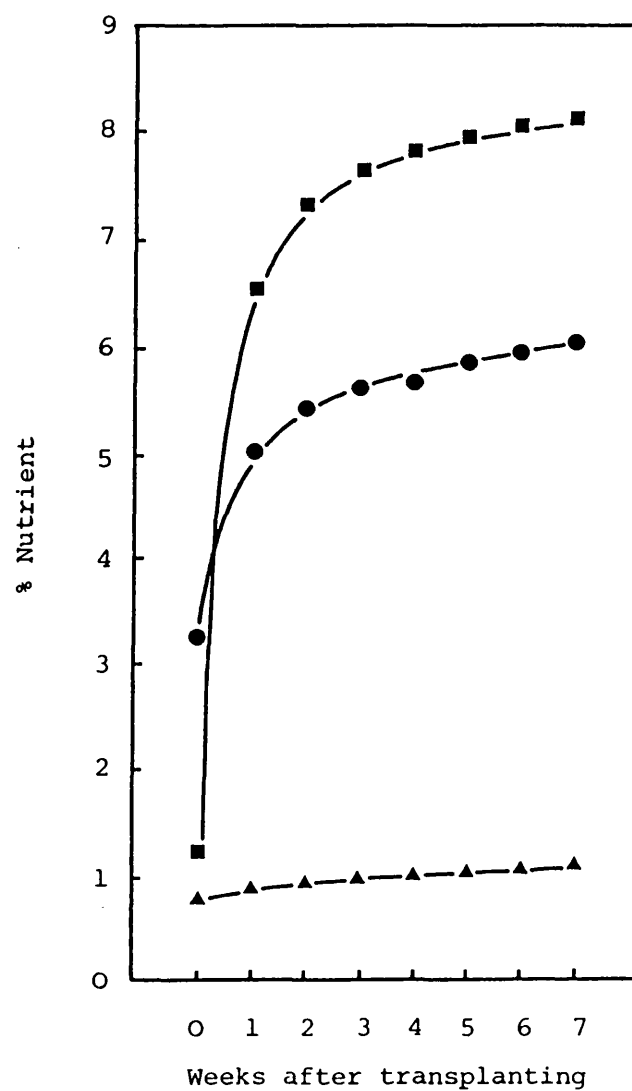
The rapid increase in percents N and K during the first week after transplanting indicates that nutrient supply during propagation may have been sub-optimal: irrigation through the mist unit (2.1.1) was based on mains water (Table 1), and nutrient levels may have been limiting to seedling growth.

This possibility has also been noted by Stevens (1974) and it is now commercial practice at Hampshire Watercress Ltd., to add supplementary nutrients through the mist unit (1.2).

Tissue mineral levels have generally been recognised as a function of stage of crop growth and physiological age of tissue (Ulrich, 1943; Ulrich and Hills, 1967; Bates, 1971), and this has been taken into account in defining critical levels.

In the present investigation, tissue mineral levels were above the critical levels (1.3) established by Robinson and Cumbus (1977) and were comparable with the shoot

Figure 16. Percentage N (●), P (▲) and K (■) in Watercress Dry Matter, in relation to Plant Age.



nutrient levels (1.3) obtained by Rothwell (1983).

Nutrient uptake was calculated on the basis of crop area ($\text{mg m}^{-2} \text{ day}^{-1}$) and results are shown in Figure 17.

As growth progressed, increasing amounts of N and K were taken up by the crop, but P absorption remained relatively constant.

Nutrient requirements vary according to stage of crop growth (Gerloff, 1963) and this may be related to the role of individual nutrients in the plant.

Nitrogen occurs in proteins, nucleic acids and many coenzymes (Sutcliffe and Baker, 1981), and its role in protein synthesis means that plant growth is strongly correlated with supply of N.

In the present investigation, watercress growth (Fig. 12) and N absorption (Fig. 17) showed similar trends, and this agrees with work reviewed by Barker and Mills (1980). Uptake of N increased with increasing growth in many species (Barker and Mills, 1980), although Adams and Winsor (1978) report that N uptake in tomato was independent of stage of growth.

Phosphorus is required for synthesising several essential phosphorylated compounds (Sutcliffe and Baker, 1981) and demand tends to remain constant throughout growth.

Phosphate absorption was independent of stage of growth

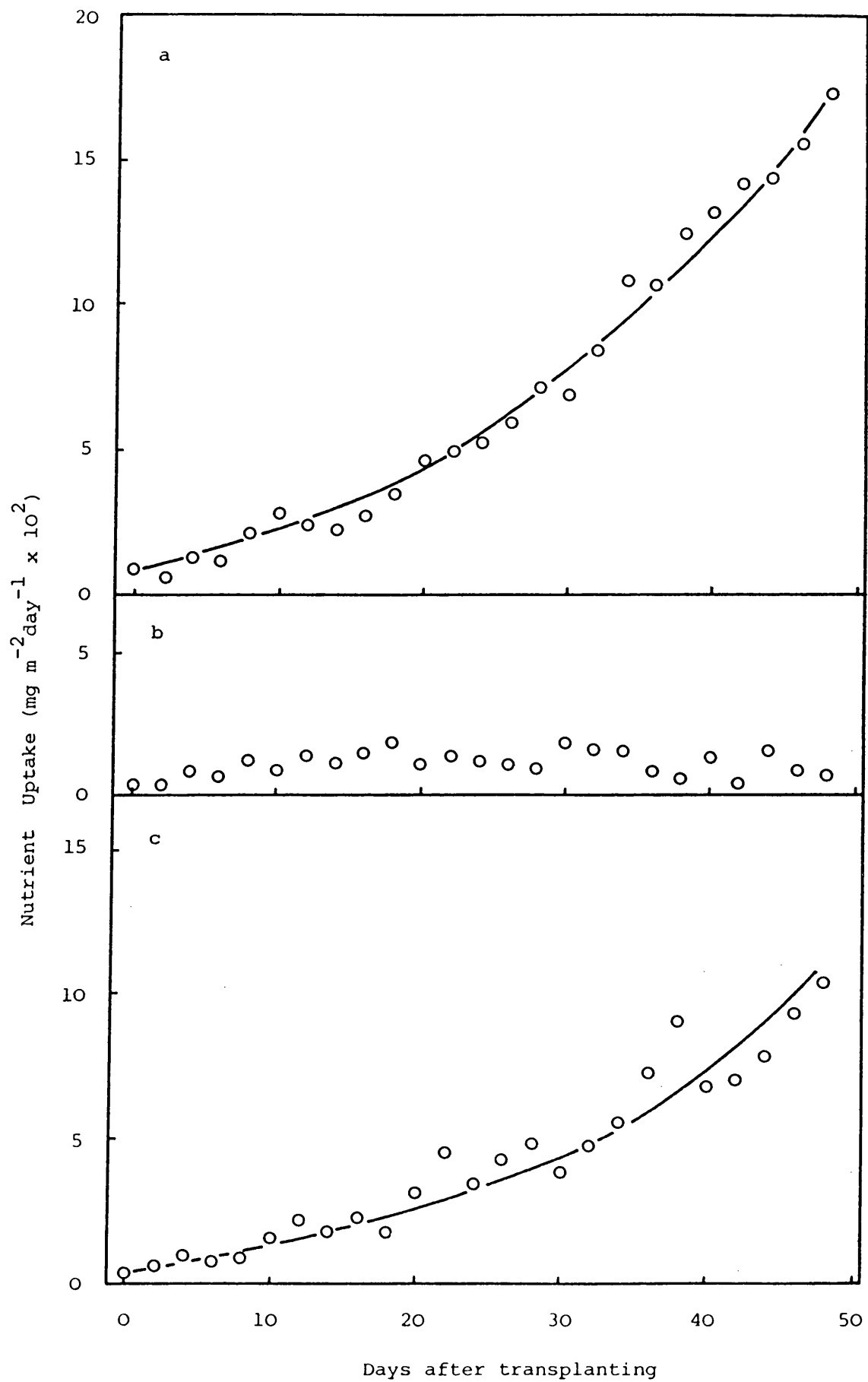
Figure 17.

Nutrient Uptake ($\text{mg m}^{-2} \text{day}^{-1}$) in
relation to Plant Age.

(a) Nitrate

(b) Phosphate

(c) Potassium.



in tomato (Adams and Winsor, 1978) and also in the present investigation (Fig. 17).

Potassium is required in relatively large quantities and plants have an almost limitless capacity for its absorption (Sutcliffe and Baker, 1981). It forms loose associations with many proteins, activates numerous enzymes and is an important osmotic regulator, involved in translocatory processes and stomatal mechanisms.

Potassium uptake by watercress (Fig. 17) was correlated with growth (Fig. 12), and a similar relationship has been observed in tomato (Adams and Winsor, 1978).

Plant growth rate and nutrient uptake are closely correlated during the vegetative growth stages of many species (Reisenauer, 1969), and tissue nutrient status is a balance between rate of uptake and growth (Cooper, 1973).

Nutrient uptake, calculated on the basis of shoot fresh weight ($\text{mg (gFW)}^{-1} \text{day}^{-1}$) is shown in Figure 18.

Measured on this basis, uptake of all three nutrients decreased as growth progressed, and this may be a function of percentage of meristematic tissue.

Meristematic tissue is involved in the metabolic control of mineral nutrients and carbohydrate reserves within the plant, and influences nutrient uptake (Williams, 1948).

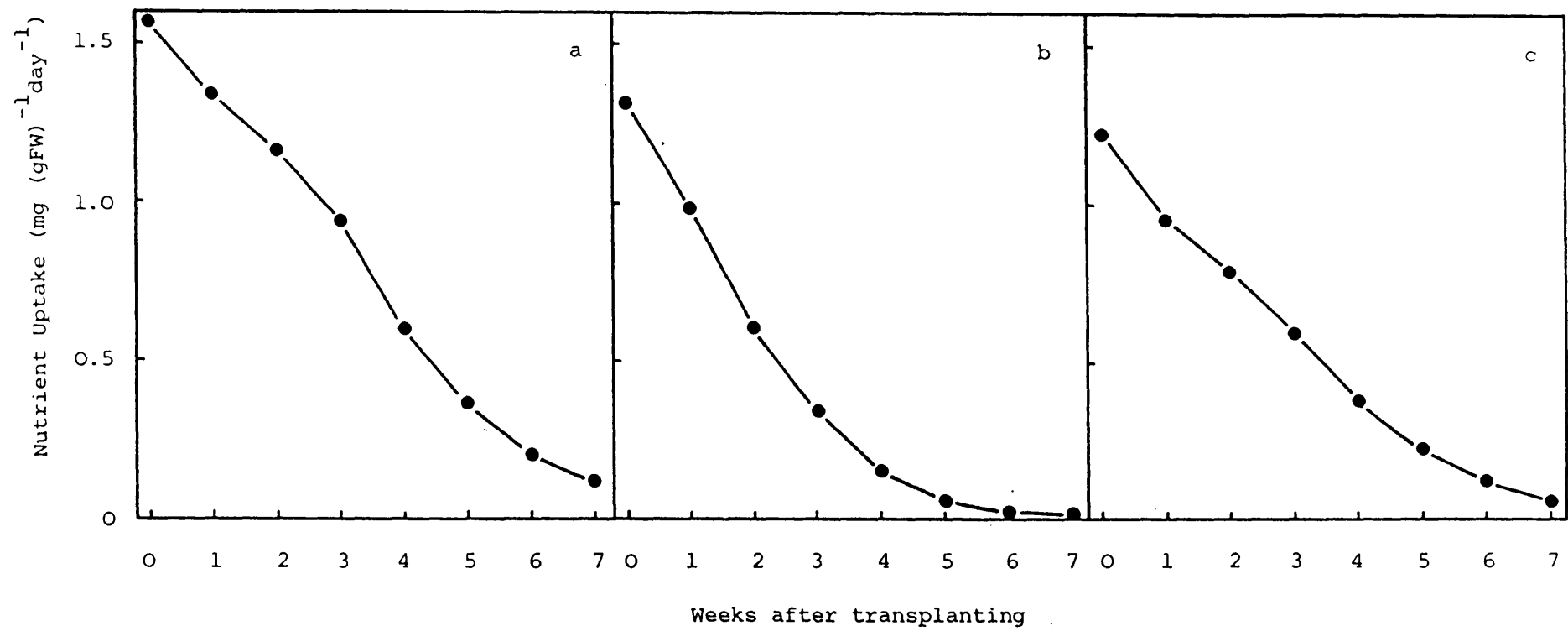
Percentage of meristematic tissue in plants is a function

Figure 18. Nutrient Uptake ($\text{mg (gFW)}^{-1}\text{day}^{-1}$)
in relation to Plant Age.

(a) Nitrate

(b) Phosphate

(c) Potassium.



of time, and decreases as growth progresses.

Nutrient flux, measured in terms of weight or volume of root, has also been seen to decrease as plant growth progresses, although roots were not measured in the present investigation (4.2.1).

In rice, Hai and Laudelout (1966) observed that P uptake per gram FW of roots decreased in older plants, but this was compensated by an increase in root weight as the plants grew. In corn (Warncke and Barber, 1974; Mengel and Barber, 1974) and barley (Clarkson *et al.*, 1978), P flux was seen to decrease as growth progressed and in ryegrass, barley and fodder radish (Woodhouse *et al.*, 1978), K flux decreased with increasing growth.

4.2.3 Summary and Conclusions

The results of the present investigation provide a quantitative appraisal of the nutrient requirements of watercress, which are seen to depend on stage of growth and on the basis used to measure uptake.

Expressed as a function of crop area, uptakes of N and K increased, while P absorption remained constant; expressed on the basis of gram FW of crop, uptake of all three nutrients decreased as growth progressed.

The actual amounts (g m^{-2}) of nutrients taken up during the 7 week period of study were:

N	35.622
P	4.658
K	23.229

giving an uptake ratio of 7.6 : 1 : 5.

The ratio of nutrients supplied to the crop was a constant 7 : 1 : 7.8, but ratio of uptake varied as growth progressed (Table 6).

The results indicate that ratio of uptake was controlled by the plant itself, rather than by the ratio of nutrients in solution and this agrees with the findings of Steiner (1980), that whatever the ratio of nutrients supplied, the plant invariably absorbs them in a pre-determined ratio which is characteristic of the plant.

Results of the present investigation indicate that optimum nutrient ratio depends on stage of plant growth.

4.3 Characterisation of the Nutrient Depletion Curves of

Watercress

Watercress has previously been cultivated under different regimes of N P and K (Cumbus, 1975), with solutions renewed every 48 h and analysed for depletion at 0 and 48 h.

Depletion was seen to depend on stage of growth, occurring more rapidly in 6-week, than in 4-week plants. Percentage reductions were calculated but nutrient depletion curves were not characterised.

Table 6. Nutrient Uptake Ratios in relation to Plant Age.

Weeks after transplanting	N P K ratio
0	1.19 : 1 : 0.92
1	1.37 : 1 : 0.96
2	2.08 : 1 : 1.31
3	2.78 : 1 : 1.74
4	4.08 : 1 : 2.57
5	6.34 : 1 : 3.92
6	11.27 : 1 : 6.88
7	31.10 : 1 : 19.38

Zones of depletion have long been known to occur round plant roots (Stiles, 1916; Trelease and Livingstone, 1922) and static cultures must be stirred to avoid localised depletion (Tidmore, 1930; Williams, 1961). Alternatively, flowing cultures may be used (Asher *et al.*, 1965; Reisenauer, 1969) while recirculated solutions allow depletion to be measured (Nye and Tinker, 1977).

4.3.1 Experimental Theory

The present investigation used a continuous depletion method (Claassen and Barber, 1974) to characterise the nutrient uptake of watercress over a range of concentrations. Plants were grown in solutions of constant volume so that decrease in solution concentration was a direct measurement of nutrient uptake. The method is well-adapted to the low concentration range and measures the concentration below which net uptake ceases.

4.3.2 Materials and Methods

Plant Material

Watercress was raised from seed and plants grown at 12 h daylength and 10°C in the controlled environment tanks (2.1.3).

Nutrient Regime

Composition of the irrigating solution was 20 : 5 : 20 mg dm⁻³ with respect to N P and K, made up in mains water

and maintained according to 2.1.5.

These concentrations were chosen, so that during depletion, each nutrient reached its minimum level after about the same time interval.

Micronutrients were replenished regularly as in 2.1.5.

Procedure

When the plants reached an average height of 25 cm, nutrient replenishment was withheld and depletion monitored.

Depletion was measured over 10 days, using a 24 h sampling interval to avoid any effects of uptake diurnality (Claassen and Barber, 1974; Rothwell, 1983).

The experimental treatments were depletion of (i) N, (ii) P and (iii) K, with all other nutrients replenished daily, and (iv) simultaneous depletion of N P and K with micro-nutrients replenished daily.

FIA was used to determine N (2.4.2) and P (2.4.1) and flame photometry to determine K levels (2.4).

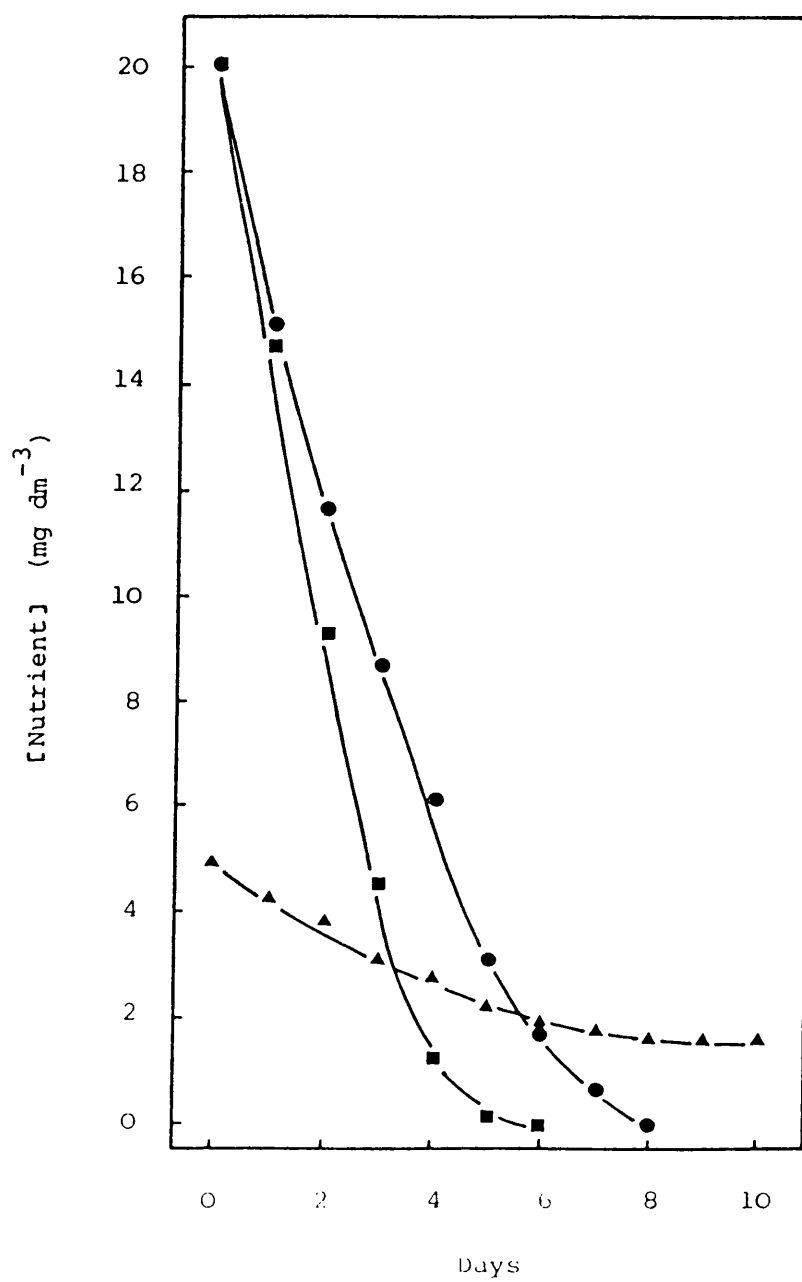
Treatments were duplicated during July - October 1985.

4.3.3 Results and Discussion

Solution concentration was taken as a measure of nutrient depletion (4.3.1) and Figure 19 shows the results of treatments i, ii and iii.

Figure 19. Solution Depletion of N (\bullet), P (\blacktriangle) and K (\blacksquare), as a function of Time.

(Treatments i, ii and iii).



(i) N Depletion

Nitrate levels fell from 20 to 0 mg dm⁻³ within 8 days and uptake rates decreased as concentrations were depleted. The concentration range of interest to watercress growers is 0 - 5 mg dm⁻³, since N concentrations in commercial irrigating supplies are of this order (Table 1). When P and K were replenished (Fig. 19), uptake of N below c. 4 mg dm⁻³ was suppressed.

(ii) P Depletion

Initial concentration of P was 4.87 mg dm⁻³ which, after 10 days without replenishment, decreased to a steady 1.7 mg dm⁻³. Uptake rate declined as the level of P in solution was depleted.

In commercial watercress beds, P levels are reported to reach 0 mg dm⁻³ in the outflow (Hampshire Watercress Ltd., pers. comm.), from irrigating waters containing c. 0.02 mg dm⁻³ P at source (Table 1).

Large fluctuations are known to occur in the mineral composition of outflow from watercress beds (Casey, 1981), and Crisp (1970) reported that significantly more P was lost in the outflow than was present in the inlet supply. This was attributed to the application of basic slag to bed bases (1.3).

In the present investigation, failure to achieve zero levels of P may have been due to the establishment of an equilibrium

between available P in solution and P precipitated as calcium phosphate. As solution-P was depleted, the calcium phosphate dissociated to maintain equilibrium concentrations of bound and soluble ions.

(iii) K Depletion

Potassium levels fell rapidly, reaching 0 mg dm^{-3} within 6 days. Uptake rates did, however, slow down as nutrient concentration was reduced, especially below *c.* 2 mg dm^{-3} . Since commercial watercress irrigating waters usually contain K levels below 2 mg dm^{-3} (Table 1), it is these low concentrations which are of interest to growers. However, depletion of a given nutrient is not usually independent of depletion of other nutrients, and Figure 20 shows the results of treatment *iv*.

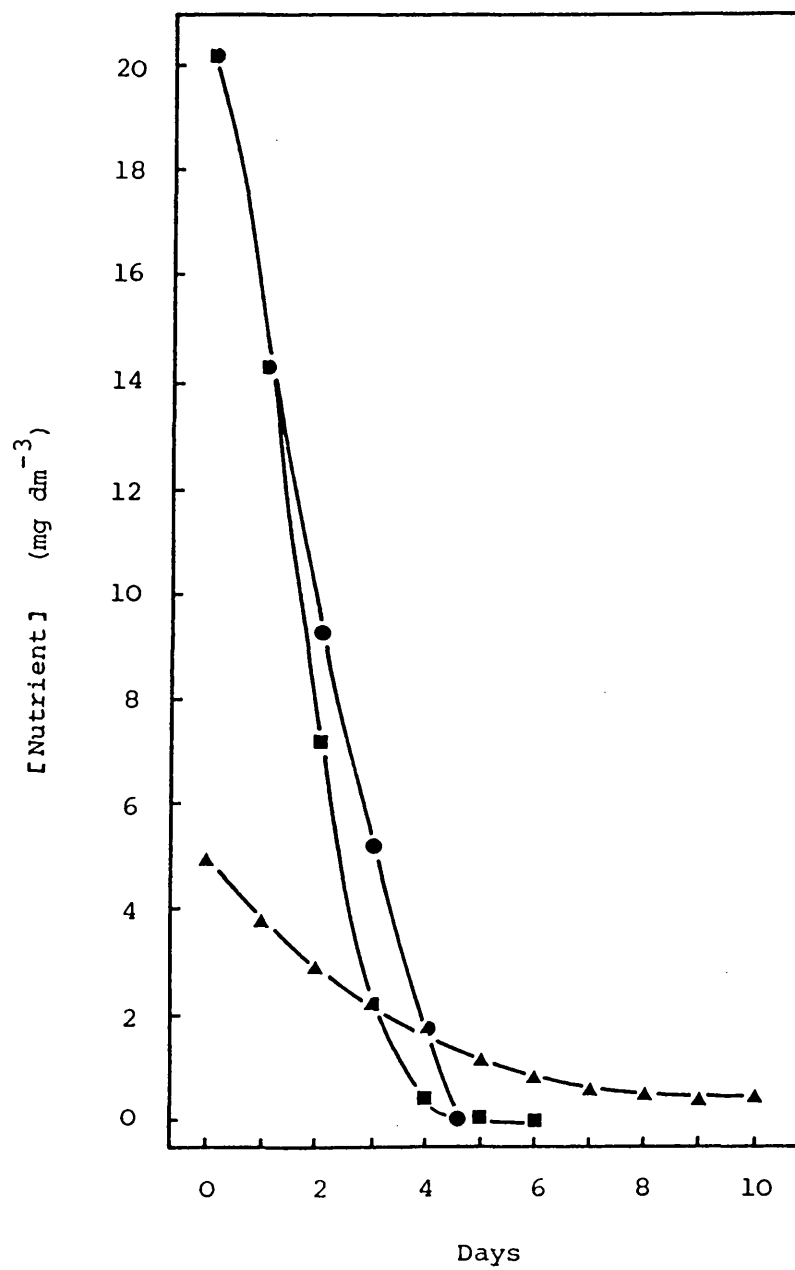
(iv) Simultaneous Depletion of N P and K

Depletion of each nutrient was more rapid when levels of all three were allowed to decline simultaneously (Figure 20), than when the two elements not under consideration were replenished (Fig. 19).

Nitrate levels fell to zero within 5 days and the concentration dependence, seen in treatment *i*, was lost.

This agrees with findings on *Lolium perenne*, that uptake of N was independent of concentration between 0.2 and 200 mg dm^{-3} (Clement *et al.*, 1978).

Figure 20. Simultaneous Depletion of N (●), P (▲) and K (■).
(Treatment iv).



Absorption of P was concentration dependent in the range studied, and this agrees with findings on eight other species by Loneragan and Asher (1967). A review by Clarkson and Hanson (1980) reports that P uptake showed more concentration-dependence than any other nutrient.

With no replenishment of N and K, P levels dropped from 4.8 to a steady 0.58 mg dm^{-3} during the depletion period. This was lower than the minimum concentration reached at constant level of N and K (Fig. 19), indicating that levels of other nutrients can affect the concentration below which net uptake ceases.

Other factors which affect this value include P status of the plant (Scheffer *et al.*, 1961), stage of growth (Jungk and Barber, 1975) and species (Christie and Moorby, 1975). In a flow-through system, flow rate is also important (Edwards and Asher, 1974), but in the present investigation both flow rate and solution volume were kept constant (2.1.3).

Potassium levels took 6 days to fall from 20 to 0 mg dm^{-3} whether N and P were replenished or not, although depletion in the range $20 - 2 \text{ mg dm}^{-3}$ was more rapid when there was no replenishment (Fig. 20).

Absorption of K was significantly reduced when levels fell below 2 mg dm^{-3} , indicating a strong concentration dependence. This has been noted in many other species (Williams, 1961;

Wild *et al.*, 1969; Young and Sims, 1972; Claassen and Barber, 1974) and a dependence on plant K status has also been reported (Johansen *et al.*, 1970).

Potassium requirements vary according to species (Bartholomew and Janssen, 1929) and plants tend to absorb more K than required for optimum growth.

The irrigating supply to commercial watercress beds (Table 1) contains *c.* 1 mg dm^{-3} K which, under experimental conditions, was seen to limit uptake. However, in a flow-through system, as in commercial watercress production, nutrient depletion is a function of flow rate (Edwards and Asher, 1974); nutrient supply may not become limiting, providing an adequate flow rate is maintained.

4.3.4 Summary and Conclusions

Using a recirculating solution, the present investigation has characterised the uptake capacity of watercress and its dependence on nutrient concentration, within the range studied.

Although uptake was measured on a time basis, the findings also reflect the situation in a commercial watercress bed, where nutrient depletion down the bed-length causes a gradient of decreasing growth.

Quantitative data cannot be extrapolated on a commercial scale, however, since nutrient depletion is also a function

of solution flow rate, which has not been investigated here.

5. SECTION C

THE INFLUENCE OF SOLUTION

COMPOSITION ON WATERCRESS GROWTH

5.1 Introduction

This series of investigations aimed to determine the extent to which solution composition affects watercress growth and subsequent yield.

Composition has been defined in terms of concentration and ratio of nutrients (Homès, 1963; Ingestad, 1970) and, to determine their relative importance in controlling yield, each must be considered separately.

To achieve maximum yield, plants must be grown in a solution comprising optimum total concentration and the optimum nutrient ratio within this total. It was these two values which the present investigation sought to identify.

5.2 Plant Growth as a Function of Solution Concentration

Previously, the cultivation of watercress under different nutrient regimes (Cumbus, 1975) has led to the determination of tissue critical levels of N P and K (1.3). Dilute nutrient solutions were used to simulate commercial watercress irrigating supplies and plant growth was also monitored as a function of solution composition. However, both concentration and ratio of nutrients were varied simultaneously (Cumbus, 1975) so their respective effects were not separately identified.

The present investigation aimed to characterise the growth response of watercress with respect to concentration, by maintaining a constant ratio of nutrients between treatments.

A solution based on that described by Hoagland and Arnon (1950) was chosen to achieve this.

Nutrient enrichment has previously given increased yields of watercress over those obtained commercially (Co'ic *et al.*, 1972), and Table 7 details the solution used.

Hydroponic solutions contain even higher nutrient levels than these, and may be 100 - 200 times more concentrated than commercial watercress supplies (Lyon and Howard, 1952). Accordingly, the present investigation used a wide range of solution concentrations, to determine that which promotes maximum yield.

5.2.1 Materials and Methods

Plant Material

Watercress seed was germinated under mist (2.1.1), then transplanted into the controlled environment tanks (2.1.3) 14 days after sowing. Plants were grown at 12 h daylength and 10°C.

Nutrient Regimes

Experimental solutions were made by supplementing mains water with Hoagland's stock solutions (Table 8), to give treatments of 5, 20, 40, 60, 80 and 100% of Hoagland's original solution (Table 9). Treatments were replicated once.

Table 7. Nutrient Concentrations (mg dm^{-3}) in the
Irrigating Solution used by Coïc *et al.* (1972).

Macronutrients		Micronutrients	
N	14.0	B	0.05
P	3.75	Cu	1.5
K	7.0	Mn	2.0
Ca	10.0	Mo	0.25
Mg	2.5	Zn	0.50
S	4.0	Fe	10.0

Table 8. Composition of the six separate stock solutions

(SS; g dm^{-3}) comprising Hoagland's 100%

nutrient solution.

Elemental composition of the solution is given

in Table 9.

Chemical compound	SS (g dm^{-3})	Volume (cm^3) of SS per dm^3 mains water
KH_2PO_4	136.091	1
KNO_3	101.100	5
$\text{Ca}(\text{NO}_3)_2$	164.096	5
MgSO_4	246.480	2
Fe-EDTA	5.000	1
H_3BO_3	2.860	}
$\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$	1.810	
$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	0.220	
$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$	0.080	
$\text{H}_2\text{MoO}_4 \cdot \text{H}_2\text{O}$	0.020	

Table 9. Elemental composition of Hoagland's 100%
nutrient solution (mg dm⁻³).

Macronutrients		Micronutrients	
N	210.12	B	0.50
P	30.98	Cu	0.02
K	234.60	Mn	0.50
Ca	200.40	Mo	0.01
Mg	48.64	Zn	0.05
S	64.13	Fe	0.60

Procedure

Solutions were sampled daily, and pH and conductance monitored (2.4). Levels of N P and K were determined (2.1.5) and solutions replenished as necessary.

At the end of the 6 week experimental period, mean plant heights were recorded and treatment yields obtained. Root and shoot weights were measured separately and the shoots then dried (2.2.1). Micro-Kjeldahl digestion (2.2.2) was used to prepare tissue samples for mineral analysis: FIA was used to measure N (2.3.2) and P (2.3.3); K was determined by flame photometry (2.3.4).

5.2.2 Results and Discussion

Figure 21 shows conductance as a function of solution concentration.

The relationship was linear in the range studied, with mains water giving a reading of $485 \mu S_{cm}^{-1}$ and treatment values maintained within the limits $\pm 5\%$.

pH was independent of concentration and remained constant throughout the experiment at 8.3 ± 0.1 .

Plant growth as a function of nutrient concentration is given in Figure 22.

Growth was expressed in terms of plant height and fresh weight, and extrapolation of the results indicated that these were maximal in the range 45 - 55% Hoagland's solution;

Figure 21. Conductance (k) as a function of Solution Concentration.

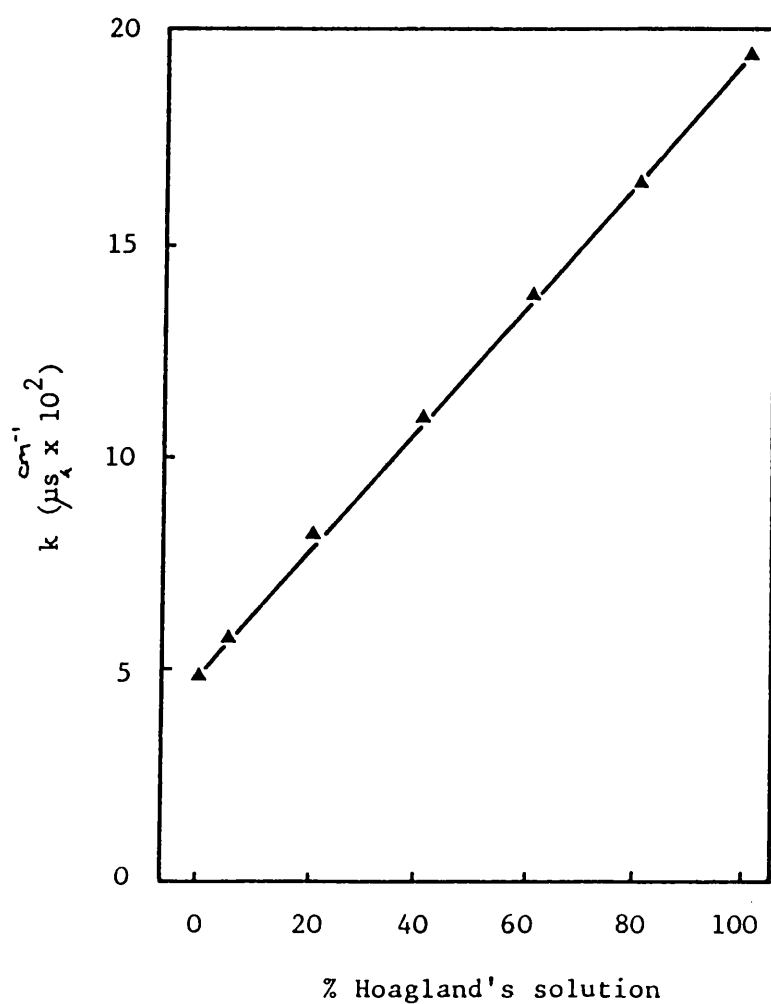
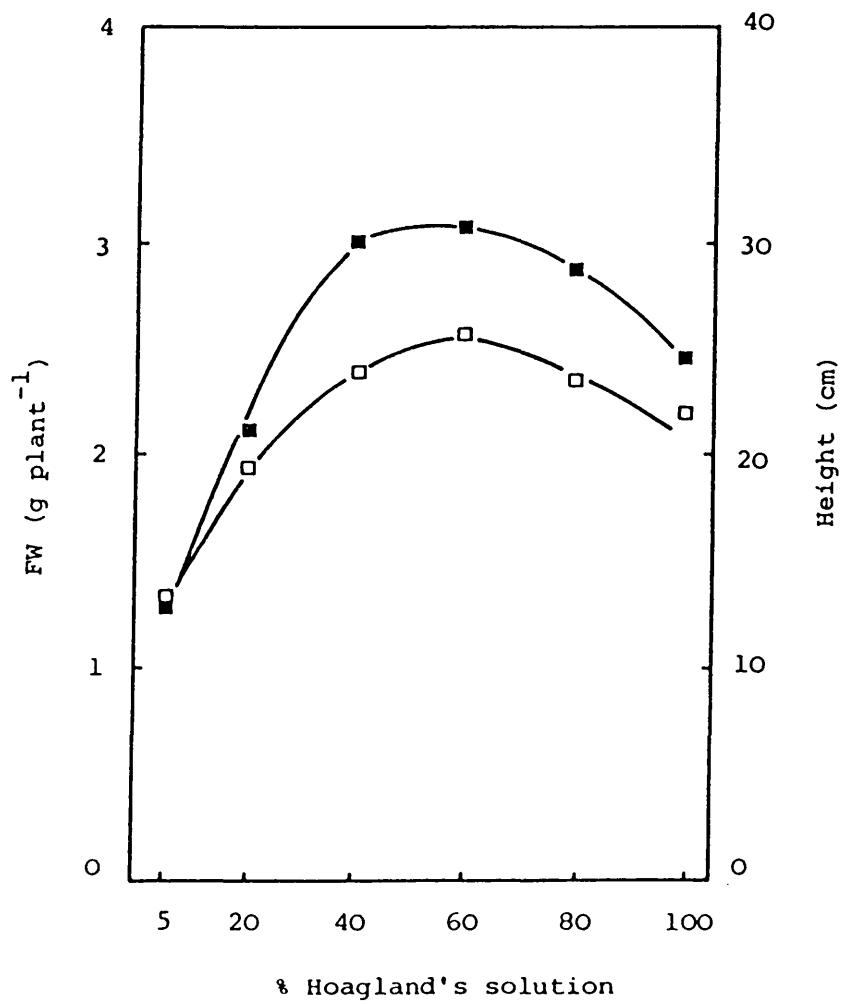


Figure 22. Plant Growth in relation to Solution Concentration :

■ Fresh weight
□ Plant height.



1150 - 1300 $\mu\text{S}_\lambda^{\text{cm}^{-1}}$ conductance (Fig. 21).

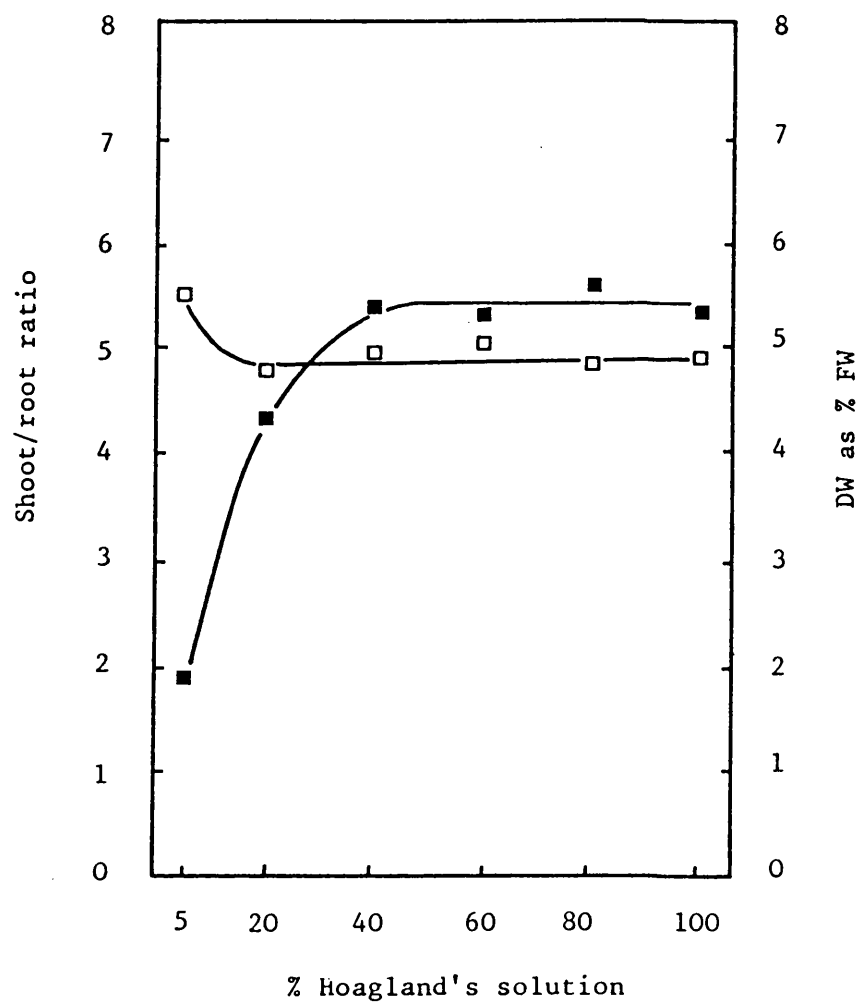
The corresponding nutrient levels (mg dm^{-3}) were calculated from Table 9:

Macronutrients		Micronutrients	
N	94 - 116	B	0.220 - 0.280
P	14 - 17	Cu	0.009 - 0.011
K	105 - 129	Mn	0.220 - 0.280
Ca	90 - 110	Mo	0.004 - 0.006
Mg	22 - 27	Zn	0.022 - 0.028
S	29 - 35	Fe	0.270 - 0.330

These concentrations are significantly higher than those (Table 7) used by Cořc *et al.* (1972), and their incorporation into commercial production would necessitate the use of a recirculating solution (Crisp, 1970). This option was originally dismissed by Crisp (1970), but commercial interest has recently been renewed by Hampshire Watercress Ltd. (pers. comm.).

Shoot/root ratio as a function of concentration is shown in Figure 23, where the low value obtained in 5% solution indicates a more extensive production of roots than shoots. This has previously been observed in plants grown in dilute nutrient solutions (Reisenauer, 1969; Ingestad and Lund, 1979), with shoot/root ratio increasing with increasing concentration (Warncke and Barber, 1973; Wild *et al.*, 1974).

Figure 23. Shoot/root Ratio (■), and Dry Weight as a percentage of Fresh Weight (□), in relation to Solution Concentration.



A stable shoot/root ratio, observed in the range 40 - 100% (Fig. 23), indicates an adequate supply of nutrients. Studies on potassium (Asher and Ozanne, 1967) have shown that increasing concentration above that required for maximum growth had little effect on yield, shoot/root ratio, % DW or tissue K content of the 14 species studied. However, it should be noted that Asher and Ozanne (1967) studied only K concentration, and nutrient ratio was not kept constant.

Dry weight as a percentage of fresh weight is also shown in Figure 23.

In the range 20 - 100%, concentration had little effect on % DW indicating that nutrient levels were sufficient; the high value obtained at 5% indicates sub-optimal nutrition (Asher and Ozanne, 1967).

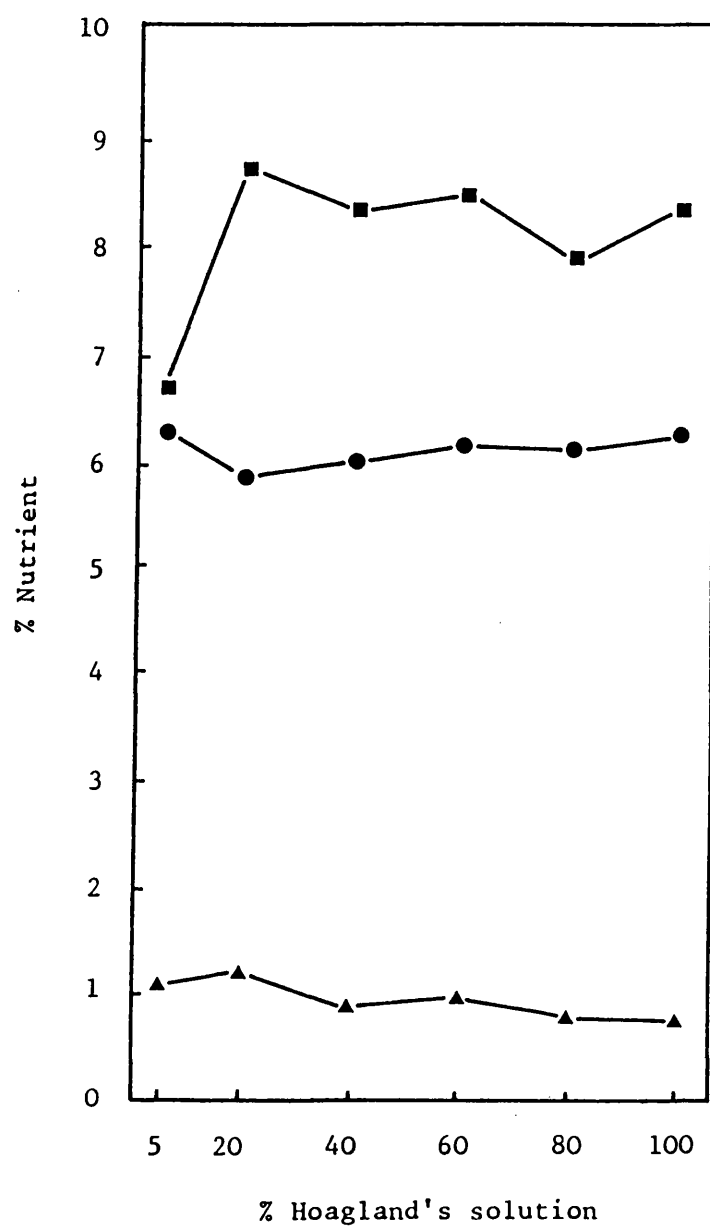
However, treatments were not all harvested at the same physiological growth stage (Fig. 22) and % DW has already been shown to depend on stage of growth (4.2.2).

Plant tissue concentrations of N P and K are shown in Figure 24.

Again, the treatments were harvested at different physiological ages (Fig. 22), making it difficult to compare results.

The relatively low K status obtained at 5% Hoagland's concentration may indicate K stress (Asher and Ozanne, 1967), but no visible deficiency symptoms were observed.

Figure 24. Percentage N (●), P (▲) and K (■) in Watercress Dry Matter, in relation to Solution Concentration.



Tissue mineral levels were above the critical levels (1.3) established by Robinson and Cumbus (1977), and were comparable with the shoot nutrient levels (1.3) obtained by Rothwell (1983).

Although nutrient uptake was monitored throughout the investigation (5.2.1), the data has not been included here. Because the plants in each treatment were growing at different rates (Fig. 22), stage of growth was not constant. Uptake differences would therefore reflect the effects of concentration on growth, and the subsequent effects of growth on uptake, rather than the direct effect of nutrient concentration on uptake.

5.2.3 Summary and Conclusions

The results of the present investigation have identified the optimum solution concentration for maximum watercress yield.

This is not necessarily the same as that for maximum nutrient uptake (Warncke and Barber, 1973) nor for maximum tissue nutrient levels (Loneragan, 1968), both of which require a different experimental approach.

It is, however, the criterion of major commercial interest, and the results indicate a potential for improving yields.

A recirculatory system would be required to allow such levels of enrichment and to prevent pollution of outflow streams (Cumbus, 1975; Casey, 1981). This would be an

expensive investment, but in view of the present findings, deserves commercial consideration.

5.3 Plant Growth with Respect to the Ratio of Nutrients in Solution

The aim of this study was to determine the optimum N P K ratio for maximum watercress growth.

An experimental approach was chosen (Homès, 1963); although a second approach also exists, which identifies the crop's optimum ratio requirements as their dry matter proportions within the plant (Ingestad, 1970; 1971).

5.3.1 Experimental Theory

The method of systematic variations (Homès, 1963) involves the variation of nutrient levels within a fixed total concentration.

For a given total amount of nutrients, optimum N P K ratio results from the coexistence of independent optimum ratios for the nutrients grouped in couples: there are two independent ratios, the third being determined by the others.

Three treatments are therefore selected, such that each of the nutrients, N P and K, appears in one treatment at high level with the other two at the same low level. When coupled, any two treatments then differ symmetrically with respect to the two elements under consideration; the third being constant.

Table 10. Theoretical proportions of N, P and K used to
study the effects of nutrient ratio on plant growth.

Treatment	Proportion			
	N	P	K	Total
i	0.666	0.166	0.166	0.999
ii	0.166	0.666	0.166	0.999
iii	0.166	0.166	0.666	0.999

$$x = 0.166 / (0.666 + 0.166)$$

$$= 0.2$$

$$1-x = 0.8$$

Nutrient levels are determined as a proportion of their sum and then expressed as fractions of this sum, denoted by x and $1 - x$. In the present investigation, proportions were 0.166 and 0.666 (Table 9), where $x = 0.2$ and $1 - x = 0.8$, corresponding to the values recommended by Homès (1963).

At the end of the experiment, treatment yields are measured and used to determine optimum N P K ratio according to the following equations.

Calculation of Results

Optimum balance for any two treatments (1 and 2) is given by

$$C_1 / (C_1 + C_2)_{\text{opt}} = Y_1 / (Y_1 + Y_2)$$

C = concentration

Y = yield

The N P K ratio, therefore, gives six separate equations:

$$N / (N + P) \quad \dots(1)$$

$$P / (N + P) \quad \dots(2)$$

$$N / (N + K) \quad \dots(3)$$

$$K / (N + K) \quad \dots(4)$$

$$K / (P + K) \quad \dots(5)$$

$$P / (P + K) \quad \dots(6)$$

where $(1) + (2) = (3) + (4) = (5) + (6) = 1$.

Optimum ratio for any two nutrients is obtained by substituting experimental yields into the appropriate equations.

5.3.2 Materials and Methods

Plant Material

Watercress seed was germinated under mist (2.1.1), then transplanted into the controlled environment tanks (2.1.4), 14 days after sowing. Plants were grown at 12 h daylength and 10°C.

Nutrient Regimes

Experimental solutions were made by supplementing mains water with the corresponding stock solutions (Table 2), so that total concentration of N P and K was 90 mg dm^{-3} . Treatment ratios are shown in Table 11.

pH was 8.2 ± 0.1 , independent of treatment, each of which was replicated twice.

Micronutrients were replenished regularly as in 2.1.5.

Procedure

Solutions were sampled daily and conductance monitored (2.4). Levels of N P and K were also determined (2.1.5) and replenished as necessary.

At the end of the 5 week experiment, treatment yields were

Table 11. Experimental nutrient variations, with respect to N, P and K, used to study the effects of ratio on watercress growth.

Treatment	Concentration (mg dm ⁻³)			Ratio		
	N	P	K	N : P	P : K	K : N
i	60	15	15	4.0	1.0	0.25
ii	15	60	15	0.25	4.0	1.0
iii	15	15	60	1.0	0.25	4.0

recorded, shoots were dried (2.2.1) and prepared for tissue analysis by micro-Kjeldahl digestion (2.2.2). FIA was used to determine N (2.3.2) and P (2.3.3), and flame photometry to measure K levels (2.3.4).

5.3.3 Results and Discussion

Table 12 shows solution conductance according to treatment.

The high-N solution (Treatment i) gave the highest conductance levels, which agrees with previous observations (Wilson, 1980) that high nitrate can cause high salinity.

The high-K treatment (iii) gave the lowest readings, while those for high-P (Treatment ii) were intermediate, but much more variable.

Mains water gave a reading of $540 \mu\text{S cm}^{-1}$ at the time of investigation.

Values for treatment yield (g plant^{-1}) are given in Table 13.

Differences between yields were small compared with the differences between treatment solutions (Table 11), suggesting that nutrient ratio is not a crucial factor determining crop yield. This agrees with observations on lettuce and tomato (Steiner, 1980), where variations in solution ratio caused no differences in yield.

Nevertheless, mean treatment yields (Table 13) were substituted into the appropriate equations (5.3.1) and used to calculate optimum N P K ratio.

Table 12. Conductance (k ; $\mu S \text{ cm}^{-1}$) as a function of nutrient ratio

Treatment	k (μS)
i	1000 ± 32.02
ii	963 ± 96.15
iii	866 ± 38.51

Table 13. Watercress yield (g plant^{-1}) as a function of nutrient ratio.

Treatment	Yield (g plant^{-1})
i	1.480 ± 0.052
ii	0.938 ± 0.026
iii	2.013 ± 0.087

Substituting the treatment yields:

$$N / (N + P) = 1.48 / 2.418 = 0.612 \quad \dots(1)$$

$$P / (N + P) = 0.938 / 2.418 = 0.388 \quad \dots(2)$$

$$N / (N + K) = 1.48 / 3.493 = 0.424 \quad \dots(3)$$

$$K / (N + K) = 2.013 / 3.493 = 0.576 \quad \dots(4)$$

$$K / (P + K) = 2.013 / 2.951 = 0.682 \quad \dots(5)$$

$$P / (P + K) = 0.938 / 2.951 = 0.318 \quad \dots(6)$$

where $(1) + (2) = (3) + (4) = (5) + (6) = 1$.

Then, equations (1) and (2) give the N : P ratio;

$$\begin{aligned} N / (N + P) &: P / (N + P) \\ &= 0.612 : 0.388 \\ &= 1.577 \end{aligned}$$

and equations (3) and (4) give the N : K ratio;

$$\begin{aligned} N / (N + K) &: K / (N + K) \\ &= 0.424 : 0.576 \\ &= 0.736 \end{aligned}$$

The K : P ratio is therefore;

$$\begin{aligned} &1.577 / 0.736 \\ &= 2.142 \end{aligned}$$

This may be checked using the third pair of equations,

(5) and (6);

$$K / (P + K) : P / (P + K)$$

$$= 0.682 : 0.318$$

$$= 2.145$$

Optimum N P K ratio for maximum watercress yield is, therefore

$$1.577 : 1 : 2.145$$

corresponding to 30 N, 19 P and 41 K within the 90 mg dm^{-3} total concentration.

However, this assumes that solution ratio controls crop yield, which may or may not be the case (Steiner, 1980). It is evident that the mathematics will give some value for optimum ratio whatever the data used, but in view of the underlying assumption, the value obtained must be treated with caution.

Table 14 shows tissue nutrient status according to treatment and also gives dry matter nutrient ratios; the criterion used by Ingestad (1970; 1971) to define optimum ratio requirements.

Dry matter ratios showed little variation with respect to treatment, suggesting that they too are controlled by the plant itself, rather than by ratio of nutrients in solution. This agrees with the results of Experiment 4.3 and the findings of Steiner (1980).

Comparing dry matter ratios (Table 14) with the values calculated from equations (1) to (6):

N : K ratio showed strong agreement; N : P and P : K ratios,

Table 14. Tissue nutrient status as a function of nutrient ratio: percentages and ratios of N,P and K.

Treatment	% Nutrient			Ratio			
	N	P	K	N : P : K	N : P	P : K	N : K
i	5.486	1.004	7.534	5.46 : 1 : 7.50	5.46	0.13	0.728
ii	5.675	1.073	6.845	5.29 : 1 : 6.38	5.29	0.16	0.829
iii	5.807	0.851	8.492	6.82 : 1 : 9.98	6.82	0.10	0.683
Mean	5.656	0.976	7.624	5.80 : 1 : 7.81	5.80	0.13	0.743

however, differed widely.

This inconsistency suggests a mathematical limitation of the method; that the optimum nutrient ratio may lie outside the range of detection.

In the present investigation, the range of variation between any pair of treatments was 0.25 - 4.0 (Table 11), and the calculation (5.3.1) did not consider values outside this range. At 5.80 and 0.13 respectively (Table 14) tissue nutrient ratios for N : P and P : K were beyond the scope of the calculation. Optimum N : K ratios, however, lay within the limits of detection.

5.3.4 Summary and Conclusions

These results have identified limitations of Homès' (1963) method of systematic variations and questioned the assumptions on which it is based.

Dry matter proportions (Ingestad, 1970; 1971) are seen to provide a more useful indication of optimum ratio requirement. Using this basis, the optimum N P K ratio for watercress nutrition may be taken as 5.80 : 1 : 7.81 (Table 14) and this compares favourably with the dry matter ratio, 5.66 : 1 : 7.64, observed in Experiment 4.2 in 5-week old plants.

Although watercress growth is seen to depend little on solution ratio of N P and K, an optimum tissue ratio does exist. This implies that if nutrients are supplied in the

ratio required, the expenditure of energy during uptake is minimal. Under such conditions, yield potential is likely to be maximal.

6. SECTION D

WATERCRESS GROWTH IN RELATION TO
SOURCE OF NITROGEN

6.1 Introduction

In preceding investigations, nitrate has been the sole source of nitrogen present in the irrigating solutions. Watercress has grown well in the absence of ammonium-N, and may actually grow better without it (Coyle *et al.*, 1972). However, yields of many species have been increased in the presence of ammonium (Reisenauer, 1978) and Tripier (1984) reports an optimal $\text{NO}_3^- : \text{NH}_4^+$ ratio of 2 : 1 for maximum watercress yield.

Early workers recognised an advantage from ammonium addition to solution cultures (Hewitt, 1952), with improved growth resulting partly from the secondary effects of solution acidification; namely the increased availability of phosphate and micronutrients (Tromp, 1962).

More recent experiments, where pH has been controlled, have also given increased yields, and Lorenz *et al.* (1972) have observed favourable growth responses in tomato, potato and canteloupe, grown under alkaline, calcareous conditions.

Ammonium-N is theoretically used more efficiently than nitrate (Reisenauer, 1978), and is less subject to leaching losses. Studies on water hyacinth, however, have identified that it is readily converted to solution nitrate (Reddy, 1983), while at high pH, ammonium volatilisation may occur. Tolerance limits to ammonium are narrow (Cox and Reisenauer, 1973), and high levels can induce ammonium toxicity. In

an all-nitrate system, however, rate of nitrate-reduction limits growth.

Optimum nitrate : ammonium ratio is therefore an important factor in the determination of maximum crop yield (Ingestad 1970; 1971), and also in the definition of optimum solution composition.

Accordingly, the present investigation sought to identify optimum nitrate : ammonium ratio for maximum watercress yield.

6.2 Experimental Theory

Neither Coïc *et al.* (1972) nor Tripier (1984) specified the ammonium compound used in their investigations, but ammonium phosphate, $\text{NH}_4\text{H}_2\text{PO}_4$, has frequently been chosen (Sutcliffe and Baker, 1981). Ammonium sulphate, $(\text{NH}_4)_2\text{SO}_4$ may also be used (Kirkby and Mengel, 1967; Warncke and Barber, 1973), and this allows independent control of phosphate levels.

In the present investigation, ammonium was provided by ammonium sulphate, with sodium nitrate supplying the nitrate (Table 2).

Determination of optimum nitrate : ammonium requirements may be achieved by one of two methods.

The first (Homès, 1963) identifies optimum ratio by a method of systematic variations within a fixed total

concentration of nitrogen (5.3.1);

the second (Cox and Reisenauer, 1977) employs a system of factorial combinations, where the level of nitrate-N is fixed and increasing levels of ammonium are added.

To establish the optimum ratio for maximum watercress yield (6.1), the first approach, variation within a fixed total concentration, was selected.

In view of the limitations of this method, however (5.3.4) a comprehensive range of ratios was investigated, encompassing the proportions 100 : 0 to 50 : 50, NO_3^- : NH_4^+ . These treatments were selected after a preliminary investigation, not reported here, determined that the highest yields were obtained from a solution containing more nitrate than ammonium.

6.3 Materials and Methods

Plant Material

Watercress seed was germinated under mist (2.1.1), then transplanted into the controlled environment tanks (2.1.3), 14 days after sowing. Plants were grown at 12 h daylength and 10°C.

Nutrient Regimes

Composition of the irrigating solution was 50 : 5 : 50 mg dm^{-3} , N P and K respectively, made up in mains water using the stock solutions detailed in Table 2.

Both nitrate and ammonium-N were supplied, to give treatments of 50 : 0, 45 : 5, 40 : 10, 35 : 15, 30 : 20 and 25 : 25 $\text{mg dm}^{-3} \text{NO}_3^- : \text{NH}_4^+$, corresponding to 100, 90, 80, 70, 60 and 50% NO_3^- with 0, 10, 20, 30, 40, 50% NH_4^+ , respectively. Micronutrients were replenished regularly (2.1.5) and the experiment was replicated once.

Procedure

Solutions were sampled daily and pH and conductance monitored (2.4). FIA was used to determine levels of NO_3^- -N (2.4.2), NH_4^+ -N (2.4.3) and P (2.4.1) and flame photometry to determine K (2.4).

Nitrification of ammonium to nitrate was observed (Reddy, 1983), so the irrigating solutions were renewed daily to maintain treatment levels.

At the end of the 5 week experimental period, mean plant heights were recorded and treatment yields obtained. Root and shoot weights were measured separately and the shoots then dried according to 2.2.1.

Micro-Kjeldahl digestion (2.2.2) was used to prepare tissue samples for mineral analysis. FIA was used to measure N (2.3.2) and P (2.3.3.) and K was determined by flame photometry.

6.4 Results and Discussion

Conductance remained constant at c. 1000 μS and pH at 8.1 ± 0.1 , irrespective of treatment.

Failure to influence pH was ascribed to the high buffering capacity of the water (2.1.5), and meant that the observed effects were due directly to nitrate : ammonium ratio, and not to any secondary effects of solution acidification (Reisenauer (1978)).

Figure 25 shows plant growth as a function of nitrate : ammonium ratio, with growth expressed in terms of plant height and fresh weight.

Extrapolation of the results indicates that growth is maximal when $\text{NO}_3^- : \text{NH}_4^+$ is 75 : 25, corresponding to a ratio of 3 : 1. This compares with the 2 : 1 ratio obtained by Tripier (1984), and contrasts with the findings of Coïc *et al.* (1972), that watercress grew better in an 'all nitrate' solution than in 6 : 1 nitrate : ammonium-N.

Both the present investigation and that of Tripier (1984) obtained maximum yield from the 80 : 20, $\text{NO}_3^- : \text{NH}_4^+$ treatment, but Tripier obtained a particularly low yield at 60 : 40, $\text{NO}_3^- : \text{NH}_4^+$ (Fig. 26).

Had this value been discounted, it would have brought the extrapolated optimum ratio even closer to the 3 : 1 obtained in the present investigation.

Shoot/root ratio as a function of $\text{NO}_3^- : \text{NH}_4^+$ is shown in Figure 27, and values tended to increase with an increase in proportion of ammonium in solution. This contrasts with

Figure 25. Plant Growth in relation to Nitrogen Source :

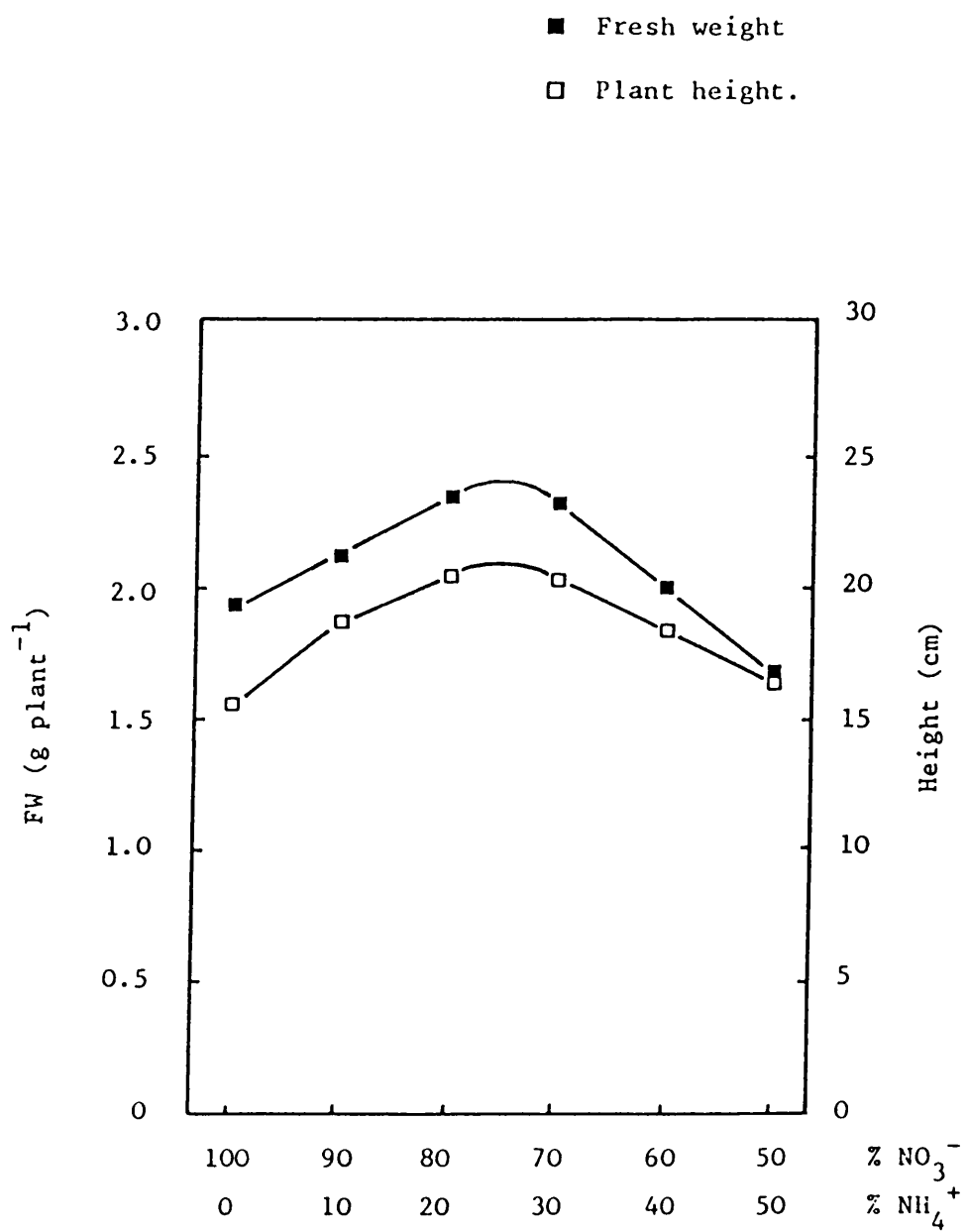


Figure 26. Watercress Yield in relation to Nitrogen
Source. Data from Tripier (1984).

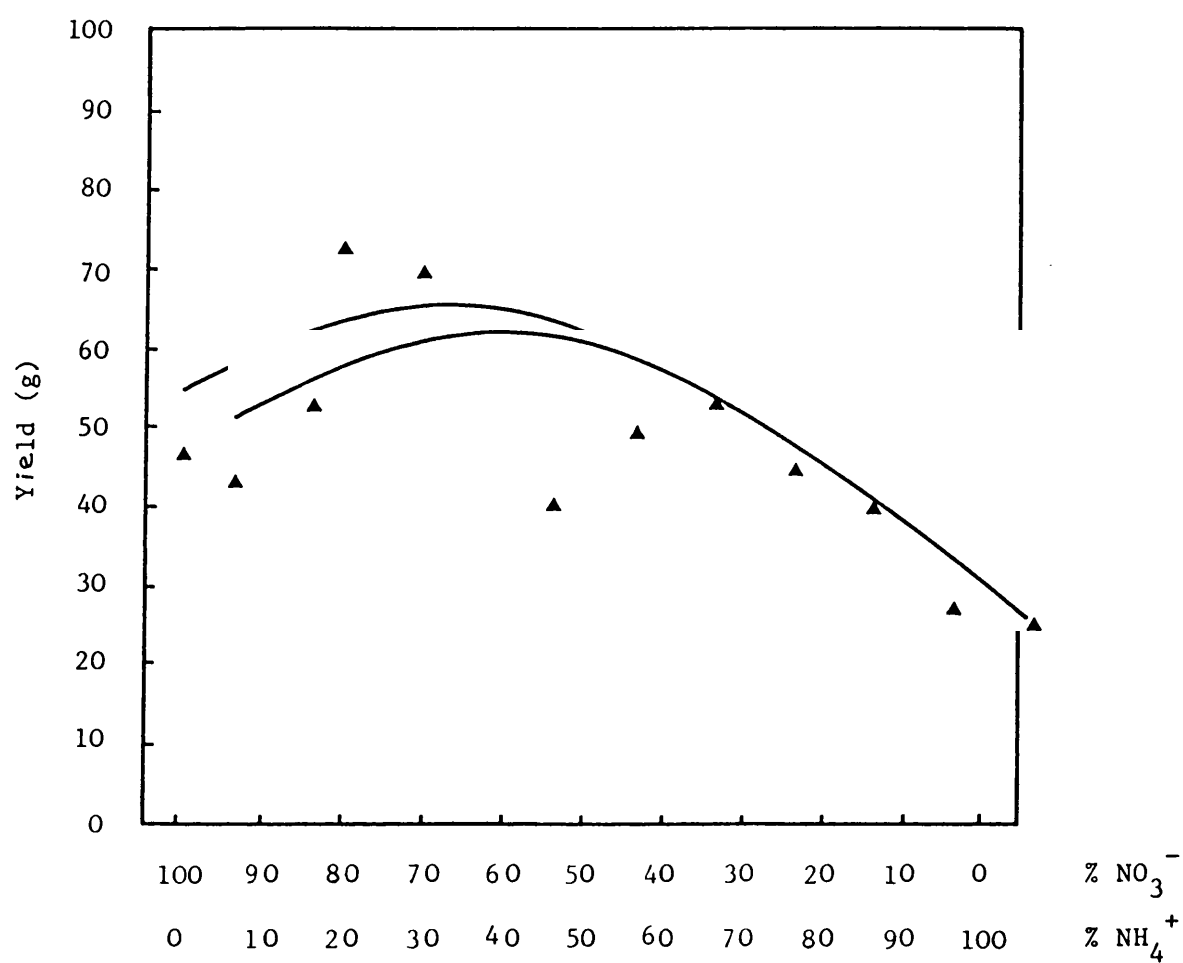
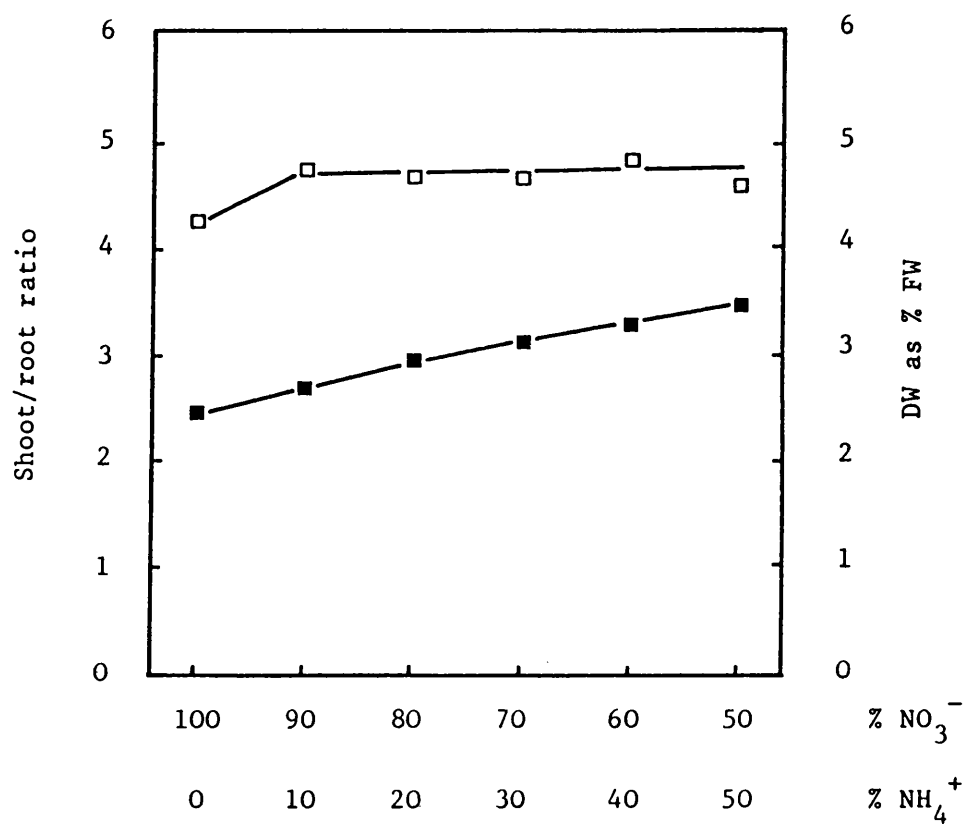


Figure 27. Shoot / root Ratio (■), and Dry Weight as a percentage of Fresh Weight (□), in relation to Nitrogen Source.



observations on corn (Warncke and Barber, 1973), where shoot/root ratio was unaffected by the proportions of nitrate and ammonium-N.

Dry weight as a percentage of fresh weight is also shown in Figure 27.

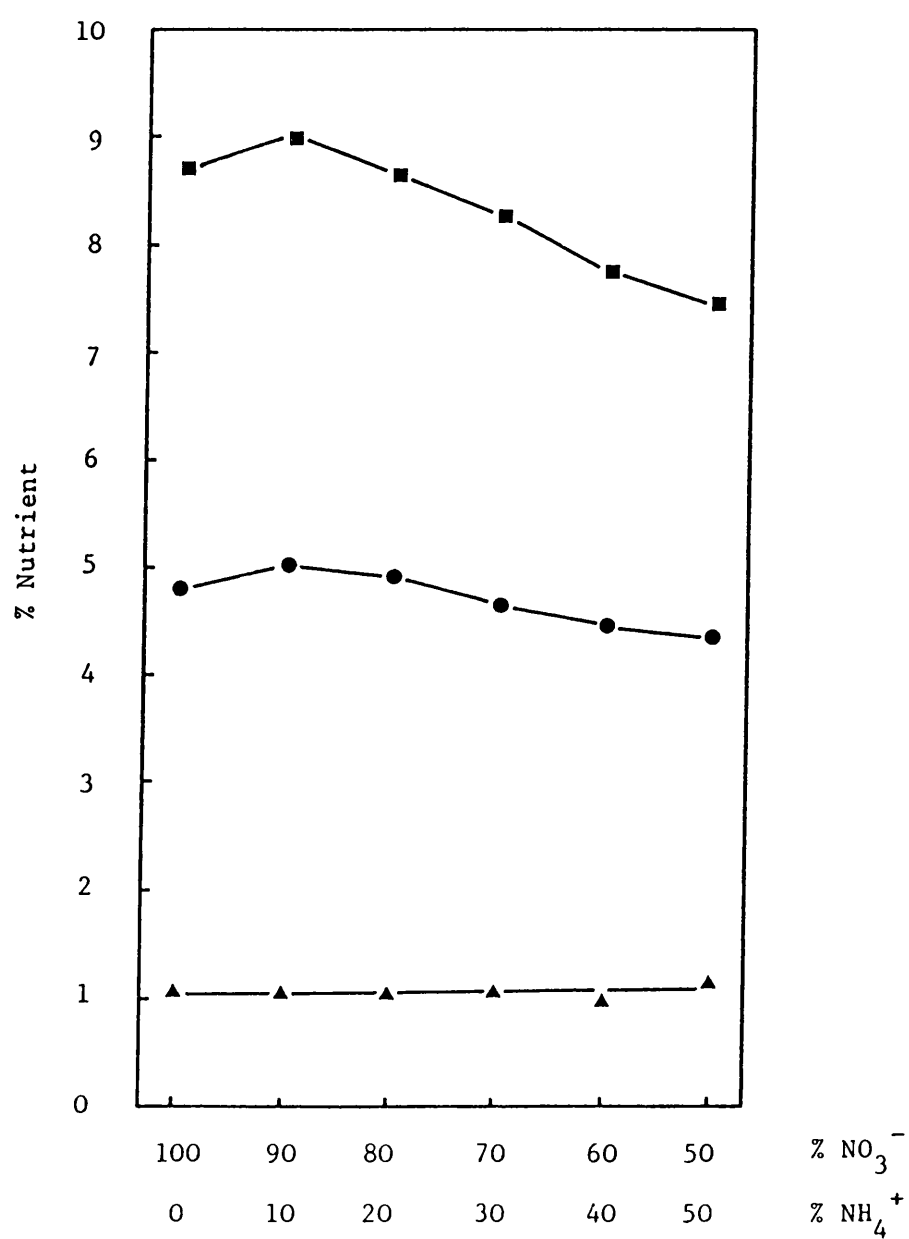
In the range 90 : 10 to 50 : 50, proportion of NO_3^- : NH_4^+ had no effect on % DW, but the lower value obtained at 100% nitrate indicates more succulent growth.

Plant tissue levels of N P and K are shown in Figure 28. Phosphate levels were independent of nitrate : ammonium ratio in the range studied, while percents N and K both showed similar trends: from the value observed at 100% nitrate, levels rose to a maximum at 90 : 10, NO_3^- : NH_4^+ , and then declined as the proportion of ammonium was increased. These observations do not conform to previously-reported interactions between source of nitrogen and tissue nutrient status, however: these are summarised in the following account.

Ammonium nutrition generally inhibits potassium accumulation due to direct K^+ / NH_4^+ competition (Tromp, 1962), which has been observed in many species (Hiatt, 1978), including watercress (Tripier, 1984). Conversely, synergism is reported between nitrate-N nutrition and K accumulation (Kirkby and Mengel, 1967; Tripier, 1984).

In the present investigation, however, correlation was ob-

Figure 28. Percentage N (●), P (▲) and K (■) in Watercress Dry Matter, in relation to Nitrogen Source.



served between tissue levels of N and K, regardless of nitrogen source.

Ammonium nutrition is also reported to stimulate P accumulation (Blair *et al.*, 1970; Hiatt, 1978; Kurvits and Kirkby, 1980), which has been attributed to anion/cation balance. However, anion/cation balance is a function of pH (Sutcliffe and Baker, 1981), so the failure in the present investigation to influence pH may account for the failure also to affect % P.

6.5 Summary and Conclusions

This work has reviewed literature concerning source of nitrogen and its effects on plant growth, morphology and nutrient status. Experimental results are discussed in relation to the findings of other workers, and maximum water-cress yield has been defined in terms of optimum nitrate : ammonium ratio.

Source of ammonium can have profound effects on plant response: Reisenauer (1978) used NH_4HCO_3 , since the HCO_3^- ion enhances K^+ accumulation, so offsetting the effects of NH_4^+ (6.4). Nitrate ions also enhance K accumulation (6.4), but NH_4NO_3 is phytotoxic (Nye and Tinker, 1977). The present investigation used $(\text{NH}_4)_2\text{SO}_4$ and NaNO_3 to provide ammonium and nitrate respectively, and this is reflected in the results. The failure of Coïc *et al.* (1972) to increase

watercress yields by adding ammonium-N may have been due to the source of ammonium used.

The investigation identified ammonium nitrification as a practical problem, which was overcome by frequent solution renewal (6.3). Nitrification inhibitors are also available, however (Hiatt, 1978), to maintain applied NH_4^+ in the ammonium form.

In a commercial situation, it is likely that nitrification would occur down the bed-length, causing the $\text{NO}_3^- : \text{NH}_4^+$ ratio to deviate from optimum and resulting in a gradient of decreasing growth. Under these circumstances, it would be worth investigating the potential use of nitrification inhibitors.

Use of such inhibitors, however, would pollute and disturb the ecological balance of outflow streams : their commercial introduction, therefore, would depend on the introduction of a recirculatory irrigating system (Section C: 5.2.3).

Traditional techniques of watercress cultivation depend on irrigation with vast quantities of spring or borehole water, supplying dilute nutrients to the crop. Intensive production, however, has led to heavy demands on these mineral nutrients and may exceed the capacity of the water to supply them. Further demands are placed on the sources supplying the irrigating water by increasing domestic and industrial use, so that growers in future may be required to reduce their consumption.

This was recognised with regard to the French watercress industry by Coïc *et al.* (1972), and highlights the need for critical evaluation of the water's nutritional and thermal properties.

A knowledge of the crop's nutrient requirements is also essential if the use of water and fertilisers is to be rationalised.

Nutrient monitoring, particularly with the recent introduction of FIA, has facilitated detailed study of watercress nutrition, and the present series of investigations has yielded valuable results. Quantitative data has been obtained, from which has been derived a basic understanding of the crop's nutrient requirements, and experiments have provided information regarding the extent to which plant growth and nutrition are controlled by environmental factors, by the plant itself and by the nutrient composition of the irrigating solution.

Environmental conditions; temperature, photoperiod and light intensity; are subject to seasonal and diurnal fluctuations, and have a marked effect on the growth and nutrient uptake of a commercially-raised crop.

The thermal input of the irrigating water has long been recognised by growers, who manipulate depth and flow-rate according to prevailing weather conditions. In this way, frost protection has been achieved, although in Summer, the water is usually cooler than the surrounding air.

This constancy in water temperature, however, may have resulted in the unwitting selection of a crop physiologically adapted to growth at *c.* 10.5°C.

The effects of temperature on crop response depend both on temperature and photoperiod, and the interactions are complex. Growth, uptake and tissue nutrient status have been quantified in relation to these interactions, while the effects of light intensity were examined separately.

Interactions between temperature and light intensity, however, are of particular concern in commercial watercress production, where the introduction of polythene protection for Winter crops has resulted in yield losses (Kapoor and Stevens, 1972). This has been ascribed to reductions in incident light intensity, which appear to outweigh the advantages gained from frost protection. Protected cropping has, however, reduced the industry's dependence on the thermal input of the irrigating water: meanwhile, the main practical consideration must be the development of a protective film with maximum transparency, to minimise light losses.

The nutritional input of the water has been extensively researched by previous workers (1.3), and crop nutrient supply is a function

of solution concentration and flow rate.

Growers adjust the water flow-rate according to plant age, and so provide increasing quantities of nutrients as growth progresses. The precise nutrient requirements of the crop, however, have not previously been quantified.

Plant nutrition is a dynamic process (Tepe and Liedenfrost, 1958), and two major determinants appear to influence plant nutrient requirements; namely the intrinsic physiology of the plant itself, and the nutritional properties of the irrigating solution.

Accordingly, watercress nutrient requirements have been quantified in relation to plant growth, and N : P : K uptake ratio was found to be a function of growth stage.

Measured on the basis of crop area, rates of N and K uptake increased as growth progressed, while P remained relatively constant. Measured on the basis of crop fresh weight, however, uptake of all three nutrients decreased as growth progressed.

Plant growth remained vegetative during the study period, and growth rate was exponential throughout this time.

Plant nutrient uptake was characterised in relation to concentration, using a continuously-depleting solution. Uptake of N was independent of concentration in the range studied; P and K uptake rates, however, showed strong dependence and were significantly reduced at the low concentrations found in commercial watercress irrigating supplies.

In the long term, solution concentration affects plant growth and nutrient uptake, which determine nutrient status and hence further growth (Nye and Tinker, 1977).

The solution which gave maximum watercress yield registered *c.* 1200 $\mu\text{S}_k^{\text{cm}^{-1}}$ conductance, and contained *c.* 100, 15 and 115 mg dm^{-3} N, P and K respectively, with corresponding concentrations of other nutrients as in Hoagland's formulation (Hoagland and Arnon, 1950). These concentrations were significantly higher than those attainable in a commercial flow-through system, and a recirculatory system was proposed to avoid nutrient pollution of outflow streams.

Introduction of a recirculating solution would reduce the requirement for large volumes of water for irrigation and nutrient supply, and would allow rational use of fertilisers. It would further permit the use of nutrient sources which have not previously been considered, due to their rapid leaching from a flow-through system. One such source is superphosphate (Barbier and Marcel, 1938), whose use would solve the industry's problems with regard to P nutrition. These became acute when the traditional phosphate source, basic slag, was lost as a result of changes in steel manufacturing processes (Rothwell, 1983).

High nutrient levels would, however, encourage algal growth, and this may reduce crop yields (Mulligan and Baranowski, 1969). A proprietary algicide included in the solution would preclude this problem, although it is not known to what extent such a product would affect crop growth.

In order to formulate stock solutions for nutrient replenishment, uptake ratios must be known (Ingestad, 1971).

Ratio of nutrients in solution was seen to have little effect on watercress growth, and optimum ratio requirements were defined as the proportions present in dry matter (Ingestad 1970; 1971). If nutrients are supplied in this ratio, therefore, the plant will expend minimum energy in their uptake from solution (Nye and Tinker, 1977; Steiner, 1980).

Ratio of nitrogen sources can significantly affect crop yield, however.

In commercial watercress production, nitrate is the sole source of nitrogen used, but experiments indicate that addition of ammonium-N can give increased yields. Using NaNO_3 and $(\text{NH}_4)_2\text{SO}_4$ to supply nitrate and ammonium respectively, a 3 : 1, NO_3^- : NH_4^+ ratio provided maximum growth.

Nutrient ionic-source influences crop response, and antagonism between NH_4^+ and K^+ , and synergism between NO_3^- and K^+ have already been reported (6.5). In tomato, Kirkby and Mengel (1967) found that K uptake was dependent on the rate of uptake of accompanying anions and similar effects, of ionic source on watercress growth and nutrition, deserve consideration.

N : P : K ratio requirements were seen earlier to depend on crop growth stage and this is also reported for nitrate : ammonium ratio, where ammonium was preferred over nitrate-N in the early

growth stages of cotton (Naftel, 1931), oat (Stahl and Shive, 1933), wheat and rice (Thelin and Beaumont, 1935) and other species (McKee, 1962).

Response to solution concentration also depends on stage of growth (Reisenauer, 1973; Shiralipour *et al.*, 1981), with optimum levels decreasing as growth progresses.

In watercress, the relations between nitrate : ammonium ratio and stage of growth, and solution concentration and stage of growth also warrant further investigation.

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